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Associations Between Brain and Behavioral Processing of Facial Expressions of Emotion and
Sensory Reactivity in Young Children

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Research Highlights

- We examine relations between brain and behavioral responses to facial expressions of emotion and temperament (i.e., sensory reactivity) in children between four to six years of age.
- Children exhibited differential early (N290) and mid-latency (P400) event-related potentials (ERPs) in response to static facial expressions of emotion.
- Individual differences in children's sensory reactivity were associated with an enhanced P400 to neutral, sad, and fearful faces.
- Children less accurately labeled neutral, sad, and fearful faces suggesting that children higher in sensory reactivity may recruit more attentional resources to decode ambiguous emotions.

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Abstract

The ability to decode and accurately identify information from facial emotions may advantage young children socially. This capacity to decode emotional information may likewise be influenced by individual differences in children's temperament. This study investigated whether sensory reactivity and perceptual awareness, two dimensions of temperament, as well as children's ability to accurately label emotions relates to the neural processing of emotional content in faces. Event related potentials (ERPs) of 4 to 6 year-old children ($N = 119$) were elicited from static displays of anger, happy, fearful, sad, and neutral emotion faces. Children, as a group, exhibited differential early (N290) and mid-latency (P400) event-related potentials (ERPs) in response to facial expressions of emotion. Individual differences in children's sensory reactivity were associated with enhanced P400 amplitudes to neutral, sad, and fearful faces. In a separate task, children were asked to provide an emotional label for the same images. Interestingly, children less accurately labeled the same neutral, sad, and fearful faces, suggesting that, contrary to previous work showing enhanced attentional processing to threatening cues (i.e., fear), children higher in sensory reactivity may deploy more attentional resources when decoding ambiguous emotional cues.

Key words: Facial emotions, face-sensitive ERPs, sensory reactivity, emotion labeling, young children

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Associations Between Brain and Behavioral Processing of Facial Expressions of Emotion and Sensory Reactivity in Young Children

Faces are a ubiquitous part of human experience and provide a unique source of information about our social world (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007). A growing literature suggests that an ability to identify and distinguish between faces begins at least as early as 3-4 days following birth (Pascalis & de Schonen, 1994; Simion & Di Giorgio, 2015) and that faces are processed uniquely from other types of items or objects (e.g., de Haan, Johnson, & Halit, 2003; Taylor, Batty, & Itier, 2004). Furthermore, signatures of face-sensitivity can be measured by event-related brain potentials (ERPs) over posterior scalp regions as early as 3 months of age (e.g., de Haan & Nelson, 1999; de Haan et al., 2003; Guy, Zieber & Richards, 2016; Peykarjou & Hoehl, 2013; Nelson, 2001; Taylor et al., 2004). In particular, several reliable ERP components have been documented to reflect structural and attentional processing of faces, possibly showing selectivity for face processing as early as the first year of life (e.g., de Haan et al., 2003; de Haan & Nelson, 1999). However, there is mixed evidence as to whether, when, and to what extent these face-sensitive ERPs and associated processes are sensitive to the emotional content in faces during development (Eimer & Holmes, 2002; Herrmann et al., 2002; Leppänen & Nelson, 2009). Furthermore, it is unclear whether individual differences in brain sensitivity may be related to individual differences in social development (e.g., Martinos, Matheson, & de Haan, 2012). To better understand the relationship between face perception and social development, we explore the relationship between brain and behavioral sensitivity to facial emotion and metrics of temperament in a large sample of young children.

Two posterior face-sensitive ERP components, the N290 and the P400, have been robustly associated with the structural processing, encoding, and attention to faces early in

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development (e.g., de Haan, et al., 2003; de Haan & Nelson, 1999). The latency of the negative going deflection recognized as the N290 in infancy decreases over development and is characterized as the N170 in older children and adults (see DeBoer, Scott, & Nelson, 2004; de Haan et al., 2003). In fact, the mature N170 is thought by some to reflect the combination of structural encoding and attentional processes associated with the infant N290 and P400 (e.g., de Haan et al., 2003). Similar functional signatures that are seen in the N290 and P400 during infancy are similarly seen in the N170 in adults (e.g., Leppänen et al., 2007). The next positive posterior ERP deflection following the N170/N290 is commonly referred to as the P400 in infants but is part of a larger complex of sustained positive deflections referred to as the Late Positive Potential (LPP) in older children and adults (see Dennis & Hajcak, 2009; Hajcak & Dennis, 2009; Olofsson et al., 2008 for reviews). Although the P400 is thought to reflect structural and attentional processing of faces in infants, the LPP is characterized as reflecting a number of face-relevant processes but most specifically, attentional processing of faces in older children and adults.

There is some evidence that face-sensitive components are also differentially sensitive to emotion content of face images from infancy. For example, Leppänen et al. (2007) found that 7-month-old infants tend to exhibit a larger P400 to fearful faces in comparison to happy faces. Similarly, Grossmann, Striano, and Friederici (2007) found differential sensitivity of ERPs between happy and angry faces in 7- and 12-month-old infants on the Nc, a negative going central component related to attention, and P400, though the pattern of sensitivity was reversed from that found by others and the pattern changed with development. Most recently, Xie and colleagues (2019) compared the processing of three types of emotion in faces (angry, fearful, and happy) across a relatively large group of 5- to 12-month-old infants, reporting some limited

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evidence of N290 responding more to fearful and happy faces compared to angry faces, and more robust evidence for larger P400s to the angry and happy faces compared to fearful faces. In older children and adults, the related N170 may show enhanced sensitivity to emotion in faces, responding more to negatively valenced emotions (i.e., fear, disgust, anger; Batty & Taylor, 2006), although this is controversial. Some have speculated that increasing sensitivity to facial expressions of emotion may be linked to on-going functional brain organization or hemispheric specialization (see Batty & Taylor, 2006; de Haan, Nelson, Gunnar, & Tout, 1998; Field, Pickens, Fox, Gonzales, & Nawrocki, 1998; Usler et al., 2020). Others, though, believe that differential sensitivity may be due to a variety of individual factors.

Specifically, prior work suggests that differential sensitivity to facial expressions of emotion may be related to individual differences in children's temperament (e.g., Martinos et al., 2012). Rothbart and Derryberry (1981) conceptualized temperament as biologically-based individual differences in reactivity and self-regulation. Individual differences in awareness of and response to sensory stimuli of varying intensity is believed to influence patterns of reactivity and self-regulation (e.g., Aron, 1999; Aron & Aron, 1997; Fox & Polak, 2004; Hsu & Porter, 2004; O'Boyle & Rothbart, 1996; Rothbart, 2012). Notably, Rothbart and colleagues distinguish between an awareness of subtle, low intensity stimulation (perceptual sensitivity) and the emotionally laden experience of discomfort in response to sensory stimulation (sensory reactivity, e.g., Putnam & Rothbart, 2006). This distinction has been questioned by some (Aron, Aron, & Jagiellowicz, 2012) but is consistent with prior work demonstrating that children's awareness of and their reaction to the sensory environment are distinct in both psychometric characteristics as well as in their corresponding relations to children's behavior (Evans, Nelson, & Porter, 2012).

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Individual differences in sensory reactivity has also long been conceptualized as a central feature in models of personality. For instance, Eysenck (1967) postulated that introverts and extroverts differ with respect to the ways they seek out or respond to sensory stimulation, with introverts thought to be more reactive to sensory stimuli while extroverts tend to seek out more sensory stimulation. These differences, Eysenck believed, were rooted in arousal mechanisms of the central nervous system.

Kagan's research on behaviorally inhibited (shy) children lends support for Eysenck's theory where extremely inhibited children have been found to exhibit heightened patterns of reactivity and autonomic arousal to unfamiliar sensory stimuli (e.g., Kagan, 1997, 2018; Kagan, Snidman, Arcus, & Reznick, 1994). Starting in infancy, Kagan (1997) has demonstrated that heightened sensory reactivity is what appears to initiate and help organize inhibited children's responses to unfamiliarity. Kagan and colleagues (1994) suggest this association reflects lower limbic thresholds and greater activation of the amygdala and hypothalamus in the face of ambiguous social cues among highly inhibited children. They further suggest that inhibited children may be biased toward detecting threats in ambiguous stimuli, leading to greater social withdrawal as a mechanism to cope with perceived threats. Though Kagan and others have emphasized that greater sensory reactivity may lead to maladaptive traits (e.g., anxiety), current understanding of sensory reactivity specifically (Aron et al., 2012) and stress reactivity in general (Belsky & Pluess, 2009) suggest that these biologically rooted aspects of temperament can make a child more susceptible to environmental influence and, therefore, be expressed as either adaptive or maladaptive depending on the availability of environmental supports.

Relatedly, prior research shows that projections from the amygdala to the occipital cortex may serve to enhance the processing of visually salient stimuli, including facial expressions of

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emotion (e.g., Amaral & Price, 1984; Eimer, Holmes, & McGlone, 2003) and especially fearful expressions (e.g., Morris et al., 1998). Given proposed links between amygdala and occipital pathways, it could be that children who are more sensory reactive (i.e., having a lower threshold for amygdala activation) may also be increasingly reactive to salient emotional cues, particularly negatively-valenced facial expressions of emotion commonly associated with threat detection (e.g., fearful or angry faces; Lazarus, 1991). Research with non-clinically anxious adults has demonstrated differential effects on posterior ERPs towards threatening information, including an enhanced N170 to fearful faces (Rossignol, Philippot, Douilliez, Crommelinck, & Campanella, 2005). Rossignol et al. (2005) speculated that the heightened N170 amplitude may result from an intensified but unconscious attentional processing of fear for anxious individuals, given that fearful expressions can signal the presence of a potential threat cue in the environment. Neuroimaging studies have likewise demonstrated differential patterns of activation among shy vs. non-shy adults across several cortical and subcortical regions to face-emotion stimuli, including fearful faces (e.g., Beaton, Schmidt, Schulkin, & Hall, 2010). An ERP study with infants showed that Nc amplitude, a marker of attentional orienting, was related to metrics of emotion regulation and emotionality, but that effects differed by the emotion type (Martinos et al., 2012). Infants with better emotion regulation had a heightened Nc response to fearful faces, whereas infants higher on the negative emotionality scale had heightened Nc responses to happy faces (Martinos et al., 2012). Together, these findings suggest that individual differences in trait characteristics may play an important role in emotion processing and relate to its brain correlates. Other results suggest this may not be the case though. For example, a recent study with 5-8-year-old children showed that the LPP, a late-going ERP index of emotional regulation, was larger for threatening faces compared to neutral faces, but only when presented

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after audio that contextualized the faces as threatening. Furthermore, the LPP response was not found to be related to measures of temperament (Usler, Foti, & Weber, 2020). Given these competing findings, there appears to be a need to further explore the role that variations in temperament may play in children's processing of facial expressions of emotions.

In the current study, we focused on two temperament traits that we suspect may influence children's neurophysiological processing of facial expressions of emotion, namely sensory reactivity and perceptual awareness. Sensory reactivity is commonly connected to heightened biobehavioral reactivity to sensory cues across a range of modalities (e.g., auditory, tactile, visual, gustatory) and is characteristic of individuals who are inhibited/anxious or shy (see Fox & Polak, 2004 for a review), whereas perceptual awareness is associated with the detection of subtle changes in the environment (e.g., Dunn, 2007; Evans et al., 2012; Putnam et al., 2001). Both dimensions likely play a role in children's responses to salient environmental cues, including social information conveyed by facial expressions of emotion. However, what is not clear from prior research is whether young children who display greater sensory reactivity show any biases in face emotion processing. If so, sensory reactive children may show differences in the response to emotion in faces as indexed by ERPs (i.e., N290, P400) relative to children who are less sensory reactive. Additionally, whether sensory reactivity is positively associated with the attentional processing of perceived threat (e.g., fearful or angry faces) remains an open question (e.g., Fu, & Pérez-Edgar, 2019). Recent work hints that individual differences in threat/non-threat discrimination may underlie some forms of anxiety-related attention bias and help explain why both perceived threat and ambiguity may similarly recruit heightened attentional processing (Dennis-Tiwary, Roy, Denefrio & Myruski, 2019). Given past findings with shy/anxious adults, we suspect that children higher on dimensions of sensory reactivity, a

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known correlate of shyness/inhibition, may show greater ERP responses to fearful and/or angry faces relative to neutral or happy faces.

Perceptual awareness has received more attention than sensory reactivity in the developmental literature on the neuroelectrophysiology of facial expression emotion processing. Jessen and Grossman (2015) have found that infants rated higher on a dimension of perceptual awareness/sensitivity showed a more positive amplitude P400 to happy faces, while infants with low perceptual awareness showed a more positive amplitude P400 to fearful faces. Jessen and Grossman (2015) went on to speculate that high perceptual sensitivity in infants may be related to attenuated perceptual thresholds, and thus, increased sensitivity for the detection of faces and differing facial expressions. However, whether the relation between perceptual awareness and face-sensitive ERPs continue beyond infancy is not entirely clear. Therefore, the current study examines the role of both sensory reactivity and perceptual awareness in relation to neurophysiological processing of facial expressions of discrete emotions among a sample of young children.

In addition to exploring the roles of sensory reactivity and perceptual awareness, respectively, and the neurophysiological processing of facial expressions beyond infancy, there is a related need to better understand children's underlying capacity to accurately identify and label emotion and whether this capacity might influence children's processing of emotional content in faces. The ability to discriminate discrete facial expressions of emotion develops relatively early, within the first six months of life (e.g., Flom & Bahrick, 2007; Izard, 1971), suggesting some degree of categorization ability. However, the capacity to accurately identify and explicitly label emotions continues to develop across early childhood (e.g., Camras & Allison, 1985; Widen & Russell, 2010). Children's emerging identification and labeling of

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emotions are thought to reflect an increasing cognitive ability for discrete categorization and appreciation of the social meaning of emotions (e.g., Izard, 1993). Prior research also suggests that emotion labeling develops from broader, valence-based categories (positive vs. negative) to more fine-grained distinctions within valence (Widen, 2013). This research suggests that children's accurate labeling of particular discrete emotions differs across emotion categories, with children first accurately labeling happy and angry faces around 3 years of age and sadness at 4 years of age, with increasingly accurate, albeit limited, labeling of fearful faces emerging around 6 years of age (see Widen, 2013, for a review). However, even with these emerging abilities, some emotions and particular instances of those emotions can remain more difficult to decode. Fear, for instance, is often poorly discriminated by even older children, with accuracy of labeling reaching only about 65% for 9-year-olds compared to happy emotional faces that reach nearly 100% accurate labeling (Widen, 2013). Given the developmental connection between understanding others' emotions and mental states (Reschke, Walle, & Dukes, 2017; Ong, Zaki, & Goodman, 2019), the capacity to identify and label emotional content of faces likely transmits an evolutionary advantage, since facial expressions of emotion can quickly communicate internal states to others that can then be used to make quick inferences and facilitate behavioral adjustments to one's environment (Gobbini, & Haxby, 2007; Izard, 1993; Öhman, 2002). At the same time, children who have difficulty with emotion perception may have difficulty understanding the social environment and appropriately adapting to their surroundings (Baron-Cohen, et al., 1999).

Interestingly, prior work suggests that children's capacity to accurately identify, decode, and label emotions may be further influenced by underlying individual differences in cognitive and/or social development (Izard, 1993). For instance, Izard and colleagues (2001) found that

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inhibition was negatively related to children's ability to recognize and accurately label emotions. While prior work has commonly framed heightened ERP responses to fearful faces as a bias towards threat detection, it is feasible, given the challenges some children face in decoding emotions, that differential responses in ERP patterns may also be related to their ability or inability to accurately identify the emotional content of faces. This may be especially the case for children higher on dimensions of sensory reactivity who tend to show heightened sensitivity to ambiguity and greater levels of behavioral inhibition (e.g., Kagan, 1997). Thus, it is possible that children who are higher in sensory reactivity and/or lower in perceptual awareness may show differential ERP responses to facial expressions of emotion, and in particular to emotions children struggle to identify, such as fear and sadness. To date, few if any studies have examined potential links between children's brain and behavioral responses to facial expressions of discrete emotions.

In sum, little research to date has examined ERP responses to emotional content in faces among younger children (i.e., four to six years of age). Even less is known about the role of individual characteristics on children's brain responses to face emotions. Finally, few studies have simultaneously measured children's ability to accurately label emotions in relation to ERP responses to emotions. In order to address these gaps, the aims of this study were to first, investigate whether face-sensitive ERPs (N290/P400) in young children 4-6 years of age distinguish between different valenced emotions (anger, happy, fearful, sad, and neutral) in static pictures of faces. Here we focus on the two ERP components shown to have face-selective functional properties, the N290 and P400 components (e.g., de Haan et al., 2003; de Haan & Nelson, 1999). Children in our sample encompassed a wide range of ages, where ERP components are changing in latency, morphology, and respective nomenclature in the literature

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(De Boer et al., 2007). Given a lack of clear consensus regarding ERP component labels for children within our age range and the observed average latency of the components in our data, we choose to use the N290/P400 nomenclature. Second, we investigated whether individual differences in two aspects of children's temperament, sensory reactivity and perceptual awareness, are related to individual differences in the brain response to emotion in faces as measured by event-related potentials. Finally, we examined how children's behavioral labeling of emotion in faces (i.e., accuracy) is related to both their brain response to discrete emotions and temperament. Given that there is little work on the brain correlates of processing face emotion and the relation to social development in young children of this age range from which to make principled a priori predictions, our study should be considered exploratory, rather than confirmatory.

Methods

Participants

Participants were drawn from a larger multifactorial study on social-emotional development ($N = 242$) from a university preschool/kindergarten located in the Western United States. Following an information meeting at the beginning of the school year, parents provided written consent for their own and their child's participation. From this larger pool of participants, 150 children were invited to participate in the ERP and emotion rating tasks using a semi-random process of selection (participants were counterbalanced to retain roughly equal numbers of girls and boys). Prior to data collection, children were given a visual and verbal description of study procedures, including an opportunity to view the laboratory and EEG equipment and ask questions about the study. Children were verbally assented prior to data collection (nine children did not assent). Thus, 141 children (68 females) completed the ERP and emotion categorization

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protocols. Mean comparisons revealed no significant differences on parent ratings of sensory reactivity or perceptual awareness for children who did or did not complete the ERP protocol. An additional 22 children (10 females) completed the ERP protocol but were excluded due to excessive artifacts in the EEG data (described below). A total of 119 (58 females) participants were retained in the final sample. Children ranged in age from 46.75 months to 81.17 months (approximately 4 to 6 years) ($M = 58.88$ months, $SD = 10.34$ months).

Demographic and behavioral data were collected from parents using Qualtrics, an online survey delivery system. Participants in the final sample were predominately White (87%) with 7% Asian/Pacific Islander, 3% Hispanic, and 3% ‘Other’ race/ethnicity, and came from intact families (94% married) with an average of 3.2 children (range = 1 to 8, $SD = 1.32$), median gross family income between \$50,000 to \$59,000 (range = less than \$10,000 to more than \$100,000), and median parent education of a four-year college degree (range = high school diploma to doctoral/professional degree). Participants in the final sample did not differ significantly on any of these demographic variables from the larger sample or from participants who were invited but not retained.

Measures

Sensory reactivity and perceptual awareness. Parents completed items from the Children’s Sensory Reactions Questionnaire (CSRQ) (Evans et al., 2012), which is a 21-item parent-report measure of children’s typical pattern of response to a number of sensory stimuli. The CSRQ scale was developed, in part, from items found on Evans and Spooner’s (2004) self-report measure and Rothbart’s parent-report measure of child temperament (*Children’s Behavior Questionnaire*: Rothbart et al., 2001). The CSRQ produces four scales, including scales for sensory reactivity and perceptual awareness (Evans et al., 2012). Parents rated items from the

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CSRQ using a seven-point scale anchored by 1 = “*extremely untrue of your child*” and 7 = “*extremely true of your child*” and included a “not applicable” option. The sensory reactivity scale consisted of five items (e.g., “my child is bothered by noises that others don't seem to notice”; “my child is bothered by bright lights that others don't seem to notice”). These items were summed with a possible range of 5 to 35 with an average score of 20.72 ($SD = 3.09$). The perceptual awareness scale includes four items (e.g., “is quickly aware of some new items in the home”, “notices when parents are wearing new clothing”) with a possible range of 5 to 28 with an average score of 21.02 ($SD = 4.26$). The internal consistencies for sensory reactivity ($\alpha = .75$) and perceptual awareness ($\alpha = .86$) were deemed acceptable and the scales were not correlated with each other ($r = -.10$, $p = .35$).

Procedures

ERPs and emotion labeling accuracy. Following assent, children completed two tasks in a laboratory located across the hall from the preschool/kindergarten classrooms: an EEG recording during passive viewing of facial expressions of emotion and a behavioral emotion-labeling task. Task order was counterbalanced across participants, with approximately half of the sample completing the emotion-labeling task first. For both protocols, emotion stimuli included static displays of angry, happy, fearful, sad, and neutral faces taken from the NimStim set of Facial Expressions developed by the Research Network on Early Experience and Brain Development (Tottenham et al., 2009). The faces of six actors displaying each of the five target emotions were selected and balanced for gender (three female), open- vs. closed-mouth displays, and included Asian, Black, and White actors. Analyses of accurate labeling did not show any actor effects across stimulus with respect to accuracy of labeling each target emotion (see Appendix A for percentage of accurate labeling for each stimulus and stimulus characteristics).

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For the *emotion labeling task*, each child rated printed versions (5"x7" color images) of the same 30 pictures used in the EEG protocol, representing five emotions from the same six actors. A trained research assistant seated across a small table from the participants (approximately 40-60 cm from the researcher) held up each picture in a random order and asked the children to identify the emotional content of each face using a simple prompt, "Is this person, happy, sad, afraid, angry, or feeling no emotions." Accurate identification of the emotion was given a score of "1" while inaccurate ratings were given a score of "0." Children's accurate ratings were summed to create an aggregate accuracy score ranging from 0 to 6 for each emotion. Children on average correctly identified 22.26 out of the 30 possible emotion faces ($SD = 4.04$, range = 8 to 30).

During the *ERP task*, the same face stimuli were presented on a monitor in a pseudo random order with the constraint that a face from each of the five emotion conditions was presented before re-randomization occurred. The stimuli were presented in the center of the screen for 500 ms. Stimuli were separated by a screen displaying a fixation cross using an interstimulus interval that varied in length randomly between 900-1200 ms to reduce anticipatory responses. Each emotion appeared 33 times for a total of 165 trials. Stimuli were presented using E-Prime 2 software (Psychology Software Tools, Sharpsburg, PA, USA) on a 17-inch computer screen with the children seated approximately 80-100 cm from the screen. The monitor was surrounded by black panels to block interfering visual stimuli in the room. A brief break was taken near the midpoint to reduce fatigue and allow the children to refocus if necessary. Children were observed throughout the protocol by a video camera mounted above the monitor. The presentation was paused if the children looked away from the monitor for more than two trials and started again once they focused again on the monitor.

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Ongoing EEG was recorded from the scalp as participants passively viewed pictures of faces using an EGI 64-Channel Hydrocel Geodesic Sensor Net and associated EEG system (Electrical Geodesics Inc., Eugene Oregon). The ongoing EEG was recorded at 250 samples per second, digitally filtered online at 0.1–100 Hz and referenced to the vertex.

The decision to separate tasks were manifold. First, we wanted to maintain comparability to previously published studies that more commonly employ passive viewing of faces during ERP tasks, especially among younger participants. Joining labeling with ERPs would likely change the nature of the task and therefore not be directly comparable to these previous studies. Second, adding an explicit task to EEG requires responses that may be harder to produce for the youngest participants in our sample, a separate behavioral rating task provided the greatest flexibility in working with all participants. Third, we wanted to reduce the possibility of introducing fatigue and potentially more artifacts during a longer EEG session while maximizing performance (e.g., attention) across both tasks.

ERP data pre-processing and reduction.

Continuous EEG data were processed off-line using NetStation 4.3.1 software (EGI, Eugene Oregon). Data were first visually examined for problematic ocular channel recordings. Problematic eye channels were marked bad and data from bad ocular channels were replaced with interpolated data from surrounding channels. After this visual inspection and replacement of problematic eye channels, raw EEG data were then lowpass filtered at 20 Hz and segmented into epochs from 200 ms before picture onset to 1000 ms after. Segmented data were then subjected to an automated artifact detection algorithm to identify and reject from further analysis epochs containing eye blinks (minimum-maximum amplitude > 200 microvolts within a window of 160 ms with 20 ms moving average in vertical eye channels), eye movements (minimum-maximum

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amplitude > 200 microvolts within a window of 160 ms with 20 ms moving average in horizontal eye channels), or too many bad/noisy channels (> 10 channels with minimum-maximum amplitude > 200 microvolts over entire segment). Channels bad in over 20% of the recording were marked bad for the entire recording and submitted to a bad channel correction algorithm using spherical spline interpolation (e.g., Ferree, 2006). Artifact-free epochs were then averaged by emotion condition for each participant, referenced to the average amplitude over the entire scalp, and baseline-corrected from the mean amplitude from -200 ms to stimulus onset. Consistent with prior research with young children (see for example Martinos et al., 2012), participants had to have 15 or more artifact free trials out of 33 total targets across each emotion category to be included in the final sample. This excluded 22 children for a final sample of 119 participants. Of these remaining participants, the average number of "good" segments for each emotion category was $M = 25.19$ ($SD = 4.55$, range 16 to 33) for happy, $M = 24.98$ ($SD = 4.56$, range 15 to 33) for sad, $M = 25.18$ ($SD = 4.51$, range 15 to 33) for neutral, $M = 24.97$ ($SD = 4.75$, range 15 to 33) for angry, and $M = 24.95$ ($SD = 4.62$, range 15 to 33) for fear. Means did not differ significantly across emotions, $F(4, 590) = .08$, $p = .99$.

Most of literature on face emotion processing is with younger infants or older children and adults and latency of the targeted components is known to change between these age groups (e.g., De Boer et al., 2007). Thus, consensus a priori standards for time windows of interest to characterize the components in our sample could not be clearly derived from existing literature. Therefore, we took a flexible data-driven approach to extracting components for analysis. Consistent with existing literature, we started with very broad time windows (150-350 ms; 250-650 ms) and a broad sampling of probable posterior electrode sites (EGI 64 channel Hydrocel electrodes: 29, 30, 31, 32, 33, 36, 38, 40, 43, 44, 47). To identify the exact time windows and

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electrode sites of interest in our data for analysis, we combined additional visual inspection and data-driven descriptive statistics from the average of all face emotion conditions together, the grand mean, as to not bias our operational definitions of the components to a particular pattern of sensitivity between emotion conditions (i.e., a collapsed localizer, Luck & Gaspelin, 2017).

The N290 was observed to be a prominent negative deflection of short duration ($M = 236$ ms, $SD = 15$ ms; see Figure 1). The P400 was observed ($M = 414$ ms, $SD = 37$ ms) to be a sustained positive deflection, with its peak emerging shortly after the N290 transition and being followed by a lesser but sustained positivity that continued to slowly subside for about 300 ms after the peak (see Figure 2). There was also substantial variability in grand mean peak latencies between participants, likely due to the wide age range of children in our sample. Based on all this information and the anticipated variation in latency due to the age range of our sample, we used adaptive time windows rather than fixed time windows to define mean amplitudes for each participant. Specifically, we defined the N290 as mean amplitude 25 ms before to 25 ms after the most negative point (i.e., peak) within a broader time window of 200- 350 ms identified for each participant and the mean ERP for each condition and the P400 as mean amplitude from 75 ms before to 75 ms after the most positive point (peak) between 350-600 ms identified for each participant and the mean ERP for each condition.

To identify the specific electrodes to use for the analysis, we extracted the grand mean amplitudes, collapsed across all conditions and averaged across all subjects during the entirety of the time windows mentioned above (200-350 ms; 350-600 ms), for each of the channels in the broad array of probable posterior sites (EGI 64 channel Hydrocel electrodes: 29, 30, 31, 32, 33, 36, 38, 40, 43, 44, 47). We then took as our target electrodes for analysis the first three contiguous sites with most negative (N290) or positive (P400) grand mean amplitudes. In the

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case of the N290, the first cluster to emerge was a left-lateralized cluster (EGI Hydrocel GSN 64 sites: Left = 29, 30, 32). For symmetry and analysis, we then took the corresponding cluster in the right hemisphere (Right = 43, 44, 47). In the case of the P400 the top three contiguous channels were a centrally-located posterior parietal cluster (Hydrocel GSN 64 Channel sites: 33, 36, 38) and there was not a need to balance symmetry (see Figure 2).

Analytic Strategy

Repeated-measures generalized mixed linear models were used to identify differences in children's N290 / P400 amplitude and emotion-labeling accuracy as a function of emotion. The models for N290 / P400 were specified with a normal distribution and an identity link function. The model for children's accuracy was specified with a Poisson distribution and a log link function. All models featured a compound symmetry covariance matrix with Restricted Maximum Likelihood (REML) and included emotion as a within-subjects factor and child age as a covariate and child gender as a control variable. Preliminary analyses including the effect of task order (ERP protocol first vs. behavioral ratings protocol first) did not change the pattern or statistical significance of the effect of emotion for all models, and thus subsequent analyses collapsed across this factor. Planned comparisons examined differences between the baseline response to neutral faces and each of the valenced emotion faces to identify patterns of emotion sensitivity. Further exploratory comparisons examined differences between emotion faces.

Separate Pearson correlations for each emotion examined associations between children's ERP responses (N290 and P400) and temperament profiles (perceptual awareness and sensory reactivity), and between children's emotion-labeling accuracy and children's age, ERP responses, and temperament profiles.

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We first report all statistics uncorrected for multiple comparisons, where the significance level (α) is $p < .05$. Additionally, for exploratory comparisons and multiple exploratory correlational analyses, we follow up to report whether significant effects survive statistical corrections for multiple comparisons using more strict Bonferroni correction thresholds (see individual analyses below for corrected thresholds). We also follow up all Pearson's correlations with Spearman's rho, a metric less sensitive to potential outlier effects (Rousselet & Pernet, 2012).

Results

Neural Processing of Face Emotions

N290. Results demonstrated a significant effect of emotion on the N290 amplitude, $F(4, 568) = 2.58, p = .037, \eta_p^2 = .02$. Planned comparisons of neutral faces with emotion faces revealed a significantly more negative N290 in response to angry faces ($M = -2.43$) compared to neutral faces ($M = -1.68$), $t(118) = -2.10, p = .038, 95\% \text{ CI } [-1.31, -0.04]$. The N290 to happy ($M = -1.57$), sad ($M = -1.47$), and fearful ($M = -1.73$) faces did not differ significantly from neutral, $ps \geq .52$. Post hoc exploration revealed a significantly more negative N290 in response to angry faces than happy faces, $t(118) = -2.61, p = .010, 95\% \text{ CI } [-1.44, -0.20]$, and sad faces, $t(118) = -2.30, p = .023, 95\% \text{ CI } [-1.64, -0.12]$. All other exploratory comparisons were not significant ($ps \geq .056$). However, none of the post-hoc exploratory contrasts survived a Bonferroni correction for multiple comparisons ($\alpha = .0083$).

P400. Results demonstrated a significant effect of emotion for the P400, $F(4, 568) = 2.48, p = .038, \eta_p^2 = .02$. Planned comparisons of the effect of emotion revealed significant differences in P400 amplitude between neutral ($M = 7.45$) and fear ($M = 8.35$), $t(118) = -2.29, p = .024, 95\% \text{ CI } [-1.73, -0.12]$, and sadness ($M = 8.36$), $t(118) = -2.24, p = .027, 95\% \text{ CI } [-1.78, -$

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0.11]. The P400 to happy ($M = 7.11$) and angry ($M = 7.79$) faces did not differ significantly from neutral, $ps \geq .60$. Post hoc exploratory comparisons revealed that P400 amplitudes in response to happy were significantly less than fear, $t(118) = -2.00$, $p = .048$, 95% CI [-2.05, -0.01] (see Figure 1). All other exploratory comparisons were not significant ($ps \geq .05$). None of the exploratory comparisons survived strict correction for multiple comparisons ($\alpha = .0083$).

Relations Between Perceptual Awareness and Sensory Reactivity and Neural Processing of Face Emotions

Perceptual awareness. No significant correlations were seen between the N290 or P400 amplitudes for any of the discrete emotion faces and perceptual awareness ($ps > .132$).

Sensory Reactivity. No significant correlations were seen between N290 amplitudes and sensory reactivity for any of the emotion conditions ($ps > .263$). However, sensory reactivity was positively correlated with P400 amplitudes for fearful ($r = .31$, $p = .003$), sad ($r = .36$, $p < .001$), and neutral faces ($r = .29$, $p = .005$), but not for happy ($r = .05$, $p = .668$) and angry ($r = .16$, $p = .123$) faces (see Figure 3). The significant correlations between sensory reactivity and P400 amplitude for neutral, sad, and fearful faces were maintained even after applying a stricter threshold for significance accounting for the multiple exploratory correlations ($\alpha = .01$). Furthermore, the same pattern of results held when Spearman's rho were computed (e.g., fearful $\rho = .31$, $p = .002$, sad $\rho = .30$, $p = .004$, neutral, $\rho = .31$, $p = .003$, happy and angry = *ns*).

Behavioral Ratings of Face Emotions

There was a significant effect of emotion on categorization accuracy, $F(4, 559) = 48.66$, $p < .001$, $\eta_p^2 = .26$. Children most accurately identified happy faces ($M = 5.70$), followed by angry ($M = 5.08$), neutral ($M = 4.22$), sad ($M = 3.88$), and fearful faces ($M = 3.31$). Planned comparisons revealed a significant difference in accuracy between neutral faces and anger,

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$t(116) = -4.23, p < .001, 95\% \text{ CI } [-1.26, -0.46]$, fear, $t(116) = 4.29, p < .001, 95\% \text{ CI } [0.50, 1.36]$, and happy, $t(116) = -7.76, p < .001, 95\% \text{ CI } [-1.86, -1.10]$. The difference in accuracy between neutral and sad faces was not statistically significant, $t(115) = 1.43, p = .16, 95\% \text{ CI } [-0.12, 0.76]$. Exploratory pairwise comparisons between anger, fear, happy, and sadness revealed significant differences between labeling of all emotion conditions ($ps \leq .006$; see Figure 4). All of these exploratory comparisons remained significant after a Bonferroni correction ($\alpha = .0083$).

Associations with Emotion-Labeling Accuracy

Age was positively associated with emotion-labeling accuracy for neutral ($r = .21, p = .022$), happy ($r = .22, p = .019$), and angry faces ($r = .31, p = .001$), but not for fearful ($r = .18, p = .051$) or sad faces ($r = -.08, p = .398$). Only the relation between age and emotion-labeling accuracy for angry remained significant following Bonferroni correction ($\alpha = .01$). N290 amplitude was negatively associated with accuracy for fearful faces only ($r = -.19, p = .040$, all other $ps \geq .238$). However, this did not remain significant after a Bonferroni correction ($\alpha = .01$). There were no relations between labeling accuracy and P400 amplitudes for any of the facial expressions of emotion (all $ps > .129$). Emotion-labeling accuracy was not correlated with sensory reactivity ($ps = .104$) or perceptual awareness ($ps = .145$). The same pattern of results held when Spearman's rho were computed, with only the correlation between age and the accurate labeling of angry faces surviving correction ($\rho = .31, p = .001$).

Discussion

The first aim of this study was to explore whether face-sensitive posterior ERPs (N290/P400) are also differentially sensitive to emotion in faces in young children and, if so, how. Similar to prior research (Batty, & Taylor, 2006; Leppänen et al., 2007), planned comparison of amplitudes did show some evidence of differentiated ERP responses to discrete

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face emotions. Specifically, higher amplitude N290 ERPs were observed in response to angry compared to neutral faces. For the later P400, greater amplitudes were also observed for fearful and sad faces compared to neutral faces. Additionally, there was some evidence that angry faces were further differentiated from happy and sad faces on the earlier N290 component and P400 amplitudes for fear were significantly higher compared to happy. However, these exploratory contrasts did not survive strict correction for multiple comparisons. Nevertheless, our group-level findings in concert with previous literature suggest that early and mid-latency ERPs are sensitive to emotional content in faces, but the particular pattern of sensitivity likely depends on contextual factors like the number of face emotions presented.

The second aim was to explore whether individual differences in aspects of children's temperament (i.e., sensory reactivity and perceptual awareness) were related to individual differences in the brain response to emotion in faces as measured by event-related potentials. We did not find any relations between perceptual awareness and ERPs. However, we did find evidence that children's sensory reactivity was related to amplitudes of the P400 in response to sad, fearful, and neutral faces. This finding extends parallel work with infants (de Haan et al., 2004; Leppänen et al., 2007; Martinos et al., 2012), children (Usher et al., 2020), and anxious adults (Rossignol et al., 2005) in several ways. Finding evidence of a relation between an elevated P400 response to fearful faces and sensory reactivity aligns with interpretations that sensory reactive children may be more sensitive to threat cues in their environment (e.g., Burris, Buss, LoBue, Pérez-Edgar, & Field, 2019; Fu, & Pérez-Edgar, 2019; Leppänen et al., 2007; Rossignol et al., 2005). Fear is thought to signal the presence of an immediate environmental threat and as such gives rise to an adaptive allocation of resources to both decode the intent of the stimuli and to organize an appropriate behavioral response (Leppänen et al., 2007). Previous

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research, however, only compared the response to fearful faces with that to positively-valenced (happy) and neutral faces. In addition to happy and neutral faces, the current study included the negatively-valenced faces of anger and sadness, enabling further examination of the relation between ERPs and temperament. If the relations between sensory reactivity and P400 amplitudes were due to an enhanced threat response in sensory-reactive children, one might expect an association between individual differences in sensory reactivity and P400 amplitude to any face conveying threat, including both fearful and angry faces (Öhman, 2002). However, we observed a relation between sensory reactivity and the brain response to fearful, sad, and neutral faces. Neutral and sad faces are generally not considered threat cues, and as such, our results may run contrary to previous interpretations (e.g., Leppänen et al., 2007). Instead, results suggest that the link between sensory reactivity and P400 amplitudes may be driven by other features of these faces besides threat. Additional confirmatory studies would be needed to substantiate this claim.

The third aim of our study, to examine behavioral labeling of face emotions in relation to ERP responses to the same faces, may suggest a novel interpretation of the association between individual differences in sensory reactivity and the brain response to facial expressions of emotion. Children's behavioral ratings of emotion faces showed that children as a group on average struggled to accurately label fearful, sad, and neutral facial expressions compared to happy and angry faces, with fearful faces being the least identified. These labeling results are consistent with findings from prior research (e.g., Widen, 2013), suggesting that fearful and sad emotions are more ambiguous to children than happy or angry faces. Furthermore, while all children as a group showed some evidence of a greater amplitude P400 to both sad and fearful faces generally, children higher in sensory reactivity appear to allocate even more brain resources to processing these three emotion conditions most ambiguous emotion categories (i.e.,

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correlations show positive relationship between sensory reactivity and P400 positivity). We suggest that this may be due to the deployment of more attentional resources to decode this ambiguity in higher sensory-reactive children compared to children considered lower in sensory reactivity (see Whalen, 1998). It is important to note that individual differences in sensory reactivity were not related to children's emotion-labeling accuracy, suggesting that sensory reactive children are not operating from a position of deficit relative to less sensory reactive children in terms of identifying and labeling emotions. The fact that neither sensory reactivity nor perceptual awareness was related to children's emotion labeling behavior may further distinguish basic sensory and attentional processing of faces reflected in our targeted ERPs (N290/P400) from the cognitive and linguistic abilities needed to explicitly identify and verbally categorize emotions. The current brain and behavioral evidence, then, may suggest a more nuanced time course of sensory, perceptual, and cognitive processes in emotion processing (Batty & Taylor, 2006; Dennis, Malone, & Chen 2009, Vuilleumier & Pourtois, 2007), with some aspects of temperament being associated with earlier sensory and/or attentional processes rather than higher-level cognitive processes downstream.

Although children more accurately labeled happy and angry faces than fearful, sadness, and neutral faces, it could be that sensory reactive children appropriated more attentional resources to these less-recognized facial expressions to engage in additional information-gathering. For instance, although facial expressions of anger and fear both convey threat (Leppänen et al., 2007), only the anger faces included an unambiguous threat source (i.e., the angry individual could lash out aggressively) whereas the fearful individuals were responding to a threat source supposedly outside the image. Furthermore, sadness is typically a well-recognized emotion among younger children (Widen, 2013), yet the coping response (i.e., approach vs.

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avoid) associated with a social partner's sadness is less clear. Indeed, even toddlers respond to an adult's sadness expressions with fewer differentiated behaviors compared to other emotions (Walle, Reschke, Camras, & Campos, 2017). Thus, our current findings may suggest that sensory reactive children are allocating additional neurological resources to decode ambiguity from salient social stimuli. The possibility remains though, that anxiety-related attention bias may lead some children to misinterpret ambiguity as a threat and further explain why both neutral faces and potentially threatening faces appear to recruit greater attentional processing (Dennis-Tiway et al., 2019). These findings may also help us understand why sensory reactive children have difficulty engaging socially with peers (Evans et al., 2012). Although speculative, it could be that sensory reactive children are more focused on processing emotional cues, especially when signals may not be entirely clear or potentially viewed as threatening. This increased allocation of resources may then compete with efforts to recruit additional neurological resources to disengage attention and to engage networks designed to initiate social behaviors.

An additional interpretation may extend from Kagan's arousability model of temperament used to explain the emergence of behavioral inhibition in young children (Kagan 1997). That is, children with a lower threshold of response, particularly in limbic systems, may respond to unfamiliarity in their environment with increased autonomic activation and sympathetic arousal, and over time they learn to withdraw from unfamiliarity in their environment. It is possible that sad and fearful faces or even the absence of emotional expression in the neutral face will be more novel to young children who are still learning the underlying meaning of discrete emotional displays (Widen, 2013). As a result, sensory reactive children may be reacting to the novelty of these less familiar face emotions rather than to their ambiguity or

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threat. Given that sensory reactivity and perceptual awareness were not associated with children's accuracy of emotion labeling likely tempers this interpretation.

While findings suggest that sensory reactive children may allocate more resources to extract information from ambiguous faces, it is interesting to note that contrary to expectations, brain responses to face emotions were not related to the dimension of perceptual awareness. These findings run contrary to earlier work of Jessen and Grossman (2014), who found that perceptual sensitivity in infants was positively related to increased P400 amplitude to happy faces, but negatively related to amplitudes for fearful faces. Although difficult to interpret null findings, it could be that as perceptually aware children mature, they become more adept at processing salient emotional cues, thus requiring less attentional processing to gather similar information from face emotions. Additional confirmatory work is needed to more fully tease apart this potential developmental course.

Limitations and Future Work

Several questions remain for future research that extend from limitations in the current study. First, little is known as to whether differentiated patterns of ERP responses to facial expressions of emotion are due to children's experience with specific expressions of emotion and the individuals expressing them. One way to test this may be to use stimuli with children's faces (e.g., LoBue & Thrasher, 2015) rather than adult faces, as children may be more likely to observe other children's displays of fear and sadness compared to adults, who may inhibit these types of emotional displays in front of children (Barrett & Campos, 1987), and thus, such displays may be less ambiguous when posed by other children. Second, additional research with more diverse samples is needed to examine the generalizability of the current findings, which were obtained in a fairly homogeneous, upper middle-class sample. Finally, emotion labeling is

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known to differ when emotional faces are presented free of context. Prior work suggests that when congruent context is added to specific images of emotional faces (e.g., a background story, bodily expressions of emotion), decoding of facial emotions is enhanced (Nelson & Mondloch, 2017; Mondloch, 2012; Widen & Russell, 2010). It would be interesting to see whether adding contextualization, thus improving identification of emotions prior to EEG data collection, would alter neurophysiological processing of emotional faces in young children. Such findings would add to an understanding about the role of experience in understanding relations between brain and behavioral processing of emotion in faces and temperament.

Conclusion

Prior work has demonstrated links between individual differences in sensory reactivity and subsequent social behaviors in children (Evans et al., 2012). Scholars have speculated that sensory reactive children may have difficulty with social interactions, in part, due to their heightened sensitivity to social stimuli and perhaps greater difficulty garnering competing neurobehavioral resources to sustain social interactions (Calkins, Gill, Johnson, & Smith, 1999; Dunn, 2001; Evans et al., 2012; Evans & Spooner, 2005). Our findings from this exploratory study provide some novel evidence of the link between heightened sensitivity to social stimuli and sensory reactivity, as children who were rated by parents as being higher in sensory reactivity show heightened neurophysiological responses to emotional faces that appear to be more ambiguous relative to children lower in sensory reactivity. It may be, then, that sensory reactive children expend more resources processing face emotion, particular in ambiguous situations, and, subsequently less resources to engage others in more complex social interactions (e.g., Evans et al., 2012). Additional confirmatory work linking brain processing to social interactions is needed to further substantiate this hypothesis.

References

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in cognitive sciences*, 4(7), 267-278. [https://doi.org/10.1016/S1364-6613\(00\)01501-1](https://doi.org/10.1016/S1364-6613(00)01501-1)
- Amaral, D. G., & Price, J. L. (1984). Amygdalo-cortical projections in the monkey (*Macaca fascicularis*). *Journal of Comparative Neurology*, 230, 465-496. <https://doi.org/10.1002/cne.902300402>
- Aron, E. N. (1999). High sensitivity as one source of fearfulness and shyness: Preliminary research and clinical implications. In L. A. Schmidt & J. Schulkin (Eds.), *Extreme Fear, Shyness, and Social Phobia: Origins, Biological Mechanisms, and Clinical Outcomes* (pp. 251-272). New York: Oxford University Press.
- Aron, E. N., & Aron, A. (1997). Sensory-processing sensitivity and its relation to introversion and emotionality. *Journal of Personality and Social Psychology Bulletin*, 73, 345-368.
- Aron, E. N., Aron, A., & Jagiellowicz, J. (2012). Sensory processing sensitivity: A review in the light of the evolution of biological responsivity. *Personality and Social Psychology Review*, 16(3), 262-282. <https://doi.org/10.1177/1088868311434213>
- Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., & Williams, S. C. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience*, 11(6), 1891-1898. <https://doi.org/10.1046/j.1460-9568.1999.00621.x>
- Barrett, K. C., & Campos, J. J. (1987). *Perspectives on emotional development II: A functionalist approach to emotions*. In J. D. Osofsky (Ed.), *Wiley Series on Personality Processes. Handbook of Infant Development* (p. 555–578). NY: John Wiley & Sons.

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Batty, M., & Taylor, M. J. (2006). The development of emotional face processing during childhood. *Developmental Science*, 9(2), 207-220. <https://doi.org/10.1111/j.1467-7687.2006.00480.x>
- Beaton, E. A., Schmidt, L. A., Schulkin, J., & Hall, G. B. (2010). Neural correlates of implicit processing of facial emotions in shy adults. *Personality and individual differences*, 49(7), 755-761. <https://doi.org/10.1016/j.paid.2010.06.021>
- Belsky, J., & Pluess, M. (2009). Beyond diathesis stress: differential susceptibility to environmental influences. *Psychological bulletin*, 135(6), 885. <https://doi.org/10.1037/a0017376>
- Burris, J. L., Buss, K., LoBue, V., Pérez-Edgar, K., & Field, A. P. (2019). Biased attention to threat and anxiety: On taking a developmental approach. *Journal of Experimental Psychopathology*, 10(3), 1-21. <https://doi.org/10.1177/2043808719860717>
- Calkins, S. D., Gill, K. L., Johnson, M. C., & Smith, C. L. (1999). Emotional reactivity and emotional regulation strategies as predictors of social behavior with peers during toddlerhood. *Social development*, 8(3), 310-334. <https://doi.org/10.1111/1467-9507.00098>
- Camras, L. A., & Allison, K. (1985). Children's understanding of emotional facial expressions and verbal labels. *Journal of Nonverbal Behavior*, 9(2), 84-94.
- DeBoer, T., Scott, L., & Nelson, C. A. (2004). Event-related potentials in developmental populations. In T. Handy (Ed.), *Event-related potentials: A methods handbook* (pp. 263–297). Cambridge, MA: MIT Press.

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- de Haan, M. (2001). The neuropsychology of face processing during infancy and childhood. In C.A. Nelson & M. Luciana (Eds.), *Handbook of Developmental Cognitive Neuroscience*. Cambridge, MA: MIT Press.
- de Haan, M., Johnson, M. H., & Halit, H. (2003). Development of face-sensitive event-related potentials during infancy: A review. *International Journal of Psychophysiology*, 51(1), 45-58. [https://doi.org/10.1016/S0167-8760\(03\)00152-1](https://doi.org/10.1016/S0167-8760(03)00152-1)
- de Haan, M., & Nelson, C. A. (1999). Brain activity differentiates face and object processing in 6-month-old infants. *Developmental Psychology*, 35(4), 1113. <https://doi.org/10.1037/0012-1649.35.4.1113>
- de Haan, M., Nelson, C. A., Gunnar, M. R., & Tout, K. A. (1998). Hemispheric differences in brain activity related to the recognition of emotional expressions by 5-year-old children. *Developmental Neuropsychology*, 14(4), 495-518. <https://doi.org/10.1080/87565649809540725>
- Dennis, T. A., & Hajcak, G. (2009). The late positive potential: A neurophysiological marker for emotion regulation in children. *Journal of child psychology and psychiatry*, 50(11), 1373-1383. <https://doi.org/10.1111/j.1469-7610.2009.02168.x>
- Dennis, T. A., Malone, M. M., & Chen, C. C. (2009). Emotional face processing and emotion regulation in children: An ERP study. *Developmental Neuropsychology*, 34(1), 85-102. <https://doi.org/10.1080/87565640802564887>
- Dennis-Tiway, T. A., Roy, A. K., Denefrio, S., & Myruski, S. (2019). Heterogeneity of the anxiety-related attention bias: A review and working model for future research. *Clinical Psychological Science*, 7(5), 879-899. <https://doi.org/10.1177/2167702619838474>

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Dunn, W. (2007). Supporting children to participate successfully in everyday life by using sensory processing knowledge. *Infants & Young Children*, 20(2), 84-101. <https://doi.org/10.1097/01.IYC.0000264477.05076.5d>
- Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport*, 13(4), 427-431.
- Eimer, M., Holmes, A., & McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cognitive, Affective, & Behavioral Neuroscience*, 3(2), 97-110.
- Evans, C. A., Nelson, L. J., & Porter, C. L. (2012). Making sense of their world: Sensory reactivity and novelty awareness as aspects of temperament and correlates of social behaviors in early childhood. *Infant and Child Development*, 21(5), 503-520. <https://doi.org/10.1002/icd.1754>
- Evans, M. A., & Spooner, A. (2004). Turn down the volume please: Self-reported sensory reactivity in shy children. *Poster presentation at the International Society of the Study of Behavioral Development, Ghent, Belgium.*
- Eysenck, H. J. (1967). *The Biological Basis of Behaviour*. Springfield, Ill.: Thomas.
- Ferree, T. C. (2006). Spherical splines and average referencing in scalp electroencephalography. *Brain Topography*, 19(1-2), 43-52. DOI: 10.1007/s10548-006-0011-0
- Field, T. M., Pickens, J., Fox, N. A., Gonzales, J. & Nawrocki, T. (1998). Facial expressions and EEG responses to happy and sad faces/voices by 3-month-old infants of depressed mothers. *British Journal Of Developmental Psychology*, 16, 485-494. <https://doi.org/10.1111/j.2044-835X.1998.tb00766.x>

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

Fu, X., & Pérez-Edgar, K. (2019). Threat-related attention bias in socioemotional development:

A critical review and methodological considerations. *Developmental Review*, 51, 31-57.

<https://doi.org/10.1016/j.dr.2018.11.002>

Flom, R., & Bahrick, L. (2007). The effects of multimodal stimulation on infants'

discrimination of affect: An examination of the intersensory redundancy hypothesis.

Developmental Psychology, 43, 238-252. <https://doi.org/10.1037/0012-1649.43.1.238>

Fox, N. A., & Polak, C. P. (2004). The role of sensory reactivity in understanding infant

temperament. In R. DelCarmen-Wiggins & A. Carter (Eds.), *Handbook of Infant,*

Toddler, and Preschool Mental Health Assessment, (pp. 105-119). Oxford University

Press.

Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces.

Neuropsychologia, 45(1), 32-41. <https://doi.org/10.1016/j.neuropsychologia.2006.04.015>

Grossmann, T., Striano, T., & Friederici, A. D. (2007). Developmental changes in infants'

processing of happy and angry facial expressions: A neurobehavioral study. *Brain and*

Cognition, 64(1), 30-41. <https://doi.org/10.1016/j.bandc.2006.10.002>

Guy, M. W., Zieber, N., & Richards, J. E. (2016). The cortical development of specialized face

processing in infancy. *Child Development*, 87(5), 1581-1600.

<https://doi.org/10.1111/cdev.12543>

Hajcak, G., & Dennis, T. A. (2009). Brain potentials during affective picture processing in

children. *Biological psychology*, 80(3), 333-338.

<https://doi.org/10.1016/j.biopsycho.2008.11.006>

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, 51(1), 59-67.
[https://doi.org/10.1016/S0006-3223\(01\)01330-0](https://doi.org/10.1016/S0006-3223(01)01330-0)
- Herrmann, M. J., Aranda, D., Ellgring, H., Mueller, T. J., Strik, W. K., Heidrich, A., & Fallgatter, A. J. (2002). Face-specific event-related potential in humans is independent from facial expression. *International Journal of Psychophysiology*, 45(3), 241-244.
[https://doi.org/10.1016/S0167-8760\(02\)00033-8](https://doi.org/10.1016/S0167-8760(02)00033-8)
- Hsu, H. & Porter, C. L. (2004). Young infants' behavioral reactivity to mild perturbation: Developmental continuity, stability, and organization. *Infancy*, 6, 95-120.
https://doi.org/10.1207/s15327078in0601_5
- Izard, C. E. (1971). The face of emotion. New York: Appleton-Century-Crofts.
- Izard, C. E. (1993). Four systems for emotion activation: Cognitive and noncognitive processes. *Psychological Review*, 100, 68-90. <https://doi.org/10.1037/0033-295X.100.1.68>
- Izard, C. E., Fine, S., Schultz, D., Mostow, A., Ackerman, B., & Youngstrom, E. (2001). Emotion knowledge as a predictor of social behavior and academic competence in children at risk. *Psychological Science*, 12(1), 18-23. <https://doi.org/10.1111/1467-9280.00304>
- Jessen, S., & Grossmann, T. (2015). Neural signatures of conscious and unconscious emotional face processing in human infants. *Cortex*, 64, 260-270.
<https://doi.org/10.1016/j.cortex.2014.11.007>
- Kagan, J. (2018). The history and theory of behavioral inhibition. In K. Pérez-Edgar & N. A. Fox (Eds.), *Behavioral Inhibition: Integrating Theory, Research, and Clinical Perspectives* (pp. 1-15). NY: Springer.

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Kagan, J. (1997). Temperament and the reactions to unfamiliarity. *Child Development*, 68, 139–143. <https://doi.org/10.1111/j.1467-8624.1997.tb01931.x>
- Kagan, J., Snidman, N., Arcus, D., & Reznick, J. S. (1994). *Galen's prophecy: Temperament in Human Nature*. NY: Basic Books.
- Lazarus, R. S. (1991). Progress on a cognitive-motivational-relational theory of emotion. *American Psychologist*, 46(8), 819.
- Leppänen, J. M., & Nelson, C. A. (2009). Tuning the developing brain to social signals of emotions. *Nature Reviews Neuroscience*, 10(1), 37-47. doi: 10.1038/nrn2554
- Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP study of emotional face processing in the adult and infant brain. *Child Development*, 78(1), 232-245. <https://doi.org/10.1111/j.1467-8624.2007.00994.x>
- LoBue, V., & Thrasher, C. (2015). The Child Affective Facial Expression (CAFE) set: Validity and reliability from untrained adults. *Frontiers in Psychology*, 5, 1532. <https://doi.org/10.3389/fpsyg.2014.01532>
- Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology*, 54(1), 146-157. <https://doi.org/10.1111/psyp.12639>
- Martinos, M. Matheson, A., & de Haan, M. (2012). Links between infant temperament and neurophysiological measures of attention to happy and fearful faces. *Journal of Child Psychology and Psychiatry*, 53(11), 1118-1127. doi:10.1111/j.1469-7610.2012.02599.x
- Mondloch, C. J. (2012). Sad or fearful? The influence of body posture on adults' and children's perception of facial displays of emotion. *Journal of Experimental Child Psychology*, 111(2), 180-196. <https://doi.org/10.1016/j.jecp.2011.08.003>

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, 383(6603), 812-815.
- Nelson, C.A. (2001). The development and neural bases of face recognition. *Infant and Child Development*, 10, 3-18. <https://doi.org/10.1002/icd.239>
- Nelson, N. L., & Mondloch, C. J. (2017). Adults' and children's perception of facial expressions is influenced by body postures even for dynamic stimuli. *Visual Cognition*, 25(4-6), 563-574. <https://doi.org/10.1080/13506285.2017.1301615>
- O'Boyle, C. G. & Rothbart, M. K. (1996). Assessment of distress to sensory stimulation in early infancy through parent report. *Journal of Reproductive and Infant Psychology*, 14, 121-131. <https://doi.org/10.1080/02646839608404509>
- Öhman, A. (2002). Automaticity and the amygdala: Nonconscious responses to emotional faces. *Current Directions in Psychological Science*, 11(2), 62-66. <https://doi.org/10.1111/1467-8721.00169>
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: an integrative review of ERP findings. *Biological Psychology*, 77(3), 247-265. <https://doi.org/10.1016/j.biopsycho.2007.11.006>
- Ong, D. C., Zaki, J., & Goodman, N. D. (2019). Computational models of emotion inference in theory of mind: A review and roadmap. *Topics in Cognitive Science*, 11(2), 338-357. <https://doi.org/10.1111/tops.12371>
- Pascalis, O. & de Schonen, S. (1994). Recognition memory in 3-to 4-day-old human neonates. *Neuroreport*, 5(14), 1721-1724. DOI: 10.1097/00001756-199409080-00008

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Peykarjou, S., & Hoehl, S. (2013). Three-month-olds' brain responses to upright and inverted faces and cars. *Developmental Neuropsychology*, 38(4), 272-280.
<https://doi.org/10.1080/87565641.2013.786719>
- Putnam, S. P., Ellis, L. K., & Rothbart, M. K. (2001). The structure of temperament from infancy through adolescence. In Elias, A. & Angleitner, A. (Eds). *Advances in Research on Temperament* (pp. 165-182). Pabst Science Publishers.
- Putnam, S. P., & Rothbart, M. K. (2006). Development of short and very short forms of the Children's Behavior Questionnaire. *Journal of personality assessment*, 87(1), 102-112.
https://doi.org/10.1207/s15327752jpa8701_09
- Reschke, P. J., Walle, E. A., & Dukes, D. (2017). Interpersonal development in infancy: The interconnectedness of emotion understanding and social cognition. *Child Development Perspectives*, 11(3), 178-183. <https://doi.org/10.1111/cdep.12230>
- Rossignol, M., Philippot, P., Douilliez, C., Crommelinck, M., & Campanella, S. (2005). The perception of fearful and happy facial expression is modulated by anxiety: an event-related potential study. *Neuroscience Letters*, 377(2), 115-120.
<https://doi.org/10.1016/j.neulet.2004.11.091>
- Rousselet, G. A., & Pernet, C. R. (2012). Improving standards in brain-behavior correlation analyses. *Frontiers in Human Neuroscience*, 6, 119.
<https://doi.org/10.3389/fnhum.2012.00119>
- Rothbart, M. K. (1981). Measurement of temperament in infancy. *Child Development*, 52, 569-578.
- Rothbart, M. K. (2012). Advances in temperament: History, concepts, and measures. In M. Zentner & R. L. Shiner (Eds.). *Handbook of Temperament*. NY, Guilford Press.

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

- Rothbart, M. K., Ahadi, S. A., Hershey, K. L., & Fisher, P. (2001). Investigations of temperament at three to seven years: The Children's Behavior Questionnaire. *Child Development, 72*(5), 1394-1408. <https://doi.org/10.1111/1467-8624.00355>
- Simion, F., & Giorgio, E. D. (2015). Face perception and processing in early infancy: Inborn predispositions and developmental changes. *Frontiers in Psychology, 6*, 969. <https://doi.org/10.3389/fpsyg.2015.00969>
- Taylor, M. J., Batty, M., & Itier, R. J. (2004). The faces of development: A review of early face processing over childhood. *Journal of Cognitive Neuroscience, 16*(8), 1426-1442. <https://doi.org/10.1162/0898929042304732>
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D. J., Westerlund, A. Casey, B.J. & Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research, 168*(3), 242-249. <https://doi.org/10.1016/j.psychres.2008.05.006>
- Usler, E., Foti, D., & Weber, C. (2020). Emotional reactivity and regulation in 5- to 8-year-old children: An ERP study of own-age face processing. *International Journal of Psychophysiology, 156*, 60-68. <https://doi.org/10.1016/j.ijpsycho.2020.07.004>
- Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. *Neuropsychologia, 45*(1), 174-194. <https://doi.org/10.1016/j.neuropsychologia.2006.06.003>
- Walle, E. A., Reschke, P. J., Camras, L. A., & Campos, J. J. (2017). Infant differential behavioral responding to discrete emotions. *Emotion, 17*(7), 1078 –1091. <https://doi.org/10.1037/emo0000307>

BRAIN AND BEHAVIORAL PROCESSING OF FACE EMOTION

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science*, 7(6), 177-188.

<https://doi.org/10.1111/1467-8721.ep10836912>

Widen, S. C. (2013). Children's interpretation of facial expressions: The long path from valence-based to specific discrete categories. *Emotion Review*, 5, 72-77.

<https://doi.org/10.1177/1754073912451492>

Widen, S. C., & Russell, J. A. (2010). Differentiation in preschooler's categories of emotion. *Emotion*, 10(5), 651-661. <https://doi.org/10.1037/a0019005>

Xie, W., McCormick, S. A., Westerlund, A., Bowman, L. C., & Nelson, C. A. (2019). Neural correlates of facial emotion processing in infancy. *Developmental Science*, 22(3), e12758.

<https://doi.org/10.1111/desc.12758>

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Figure 1. Event-related potentials to different face emotions A). Average waveform over lateralized posterior scalp sites. B). Mean N290 amplitude for each emotion type. C). Average scalp topography between 200-250 ms. White dots represent electrode sites used in analysis.

Figure 2. Event-related potentials to different face emotions A). Average waveform over central posterior scalp sites. B). Mean P400 amplitude for each emotion type. C). Average scalp topography between 350-400 ms. White dots represent electrode sites used in analysis.

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Figure 3. Scatterplots of relations between sensory reactivity and neural processing of face emotion.

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Figure 4. Estimated marginal means of children's emotion-labeling accuracy. The maximum possible score was 6. Error bars represent +/- 1 SE. All mean differences were statistically significant at the $p < .01$ level with the exception of Neutral and Sad, $p = .16$.