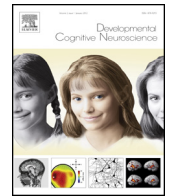




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## Editorial

# Contributions of social and affective neuroscience to our understanding of typical and atypical development



## 1. Introduction

The study of typical and atypical development in children and adolescents has become increasingly informed by and integrated with social and affective neuroscience perspectives. Emerging research from the social and affective neurosciences highlights the influence of social and emotional factors, and their interactions, on the developing brain. The purpose of this special section is to draw attention to the rich contributions to developmental cognitive neuroscience that are emerging from social and affective science research, and to stimulate additional future research in these areas. The papers in this special issue were drawn from research presented at two recent scientific meetings. The first meeting, held in June of 2012 at the University of Maryland, was organized as part of the charge from the new NSF-funded Maryland Neuroimaging Center. The focus of the meeting was on developmental social neuroscience, including the development of face processing, reward processing, and social cognition. The second meeting was the Developmental Affective Neuroscience Symposium held at the University of Pittsburgh in September of 2012, which highlighted social and affective neuroscience research on the development of positive affect systems. Both meetings attracted an international group of researchers interested in using tools such as fMRI and EEG to document social and emotional influences on normative development and implications for atypical social and emotional development.

Many of the papers in this special section address questions within a developmental psychopathology frame. This theoretical perspective promotes mutually

informative research on both typical and atypical development as a way to understand how basic developmental processes can lead to both adaptive and maladaptive outcomes (Cicchetti, 1989). This approach recognizes that development is nested within both biological and social contexts, and ultimately aims to chart how the dynamic interplay of biological, social, emotional, and cultural influences shape developmental trajectories (Cicchetti & Toth, 1998). As such, the papers in this special section reflect the full range of developmental processes, with half of the papers focusing on normative neurodevelopment within typically developing youth, and the other half focusing on how neurodevelopment is altered in youth with, or are at high risk for, various forms of psychopathology. Papers in the current issue focus primarily on forms of developmental psychopathology that are thought to be characterized by altered social and emotional processing, such as autism spectrum disorders (Luyster, Powell, Tager-Flusberg, Nelson; Vander Wyk, Hoffmann, & Pelphrey) anxiety disorders (Caouette & Guyer; Ernst et al.), and mood disorders (Thomas et al.; Olinio et al.). Papers also tend to focus on transitional periods of development, such as infancy (Luyster et al.; Nelson, Righi, Westerlund & Cogdon), early childhood (Rice, Viscomi, Riggins, Redcay), and adolescence (Whittle et al.; Spielberg, Olinio, Forbes, & Dahl; Ernst et al.; Casement et al.; Caouette & Guyer; Olinio et al.; Jankowski et al.; Perlman, Hein & Stepp, Tan et al.), which are often considered key developmental windows for socio-affective influence (Calkins & Bell, 1999). We have organized the papers to highlight four themes that characterize current and emerging research in developmental and social affective neuroscience. These include (1) The effects of social context (i.e. parents and peers) on brain structure and function in regions of the brain that support socio-affective behavior; (2) the role of reward and threat circuits (and their interactions) in developmental psychopathology (3) the need to

investigate emotion-cognition interactions in developmental psychopathology, and (4) efforts to chart the early typical and atypical development of socio-affective processing. Throughout this editorial, references to papers from the current issue will be presented in bold.

## 2. Theme 1: Effects of social context on brain structure and function in regions of the brain that support socio-affective behavior

A widely accepted principle in developmental psychology is that children's social environments play a fundamental role in shaping their emotional health and development. However, little is understood about how the quality of social relationships, such as parent-child and peer relationships, influences the neural systems that support adaptive emotional development. Four of the papers in this special section address the question of how parenting and peer relationships “get inside the brain.” While most studies on contextual influences on the brain have focused on children exposed to extreme environmental conditions such as maltreatment and neglect (Belsky & de Haan, 2011), the papers in this special section focus on how brain structure and function vary in association with a more normative range of social experiences, such as variations in parental warmth. For example, in one of the first studies to examine how positive aspects of the social environment are associated with longitudinal measures of brain development, Whittle et al. show that positive maternal parenting observed at age 12 is associated with structural changes in limbic-striatal brain regions over the next four years. Specifically, warm and supportive parenting by mothers is associated with a lower rate of volumetric growth in the amygdala and accelerated cortical thinning in the orbitofrontal cortices from ages 12 to 16. Whittle et al. argue that these changes represent “exaggerations of the normative pattern of growth” (insert page # here) that are typically associated with lower rates of psychopathology and more optimal social and emotional functioning.

Casement et al. also use longitudinal data to examine the effects of parental warmth in early adolescence (ages 11–12) on brain development, but focus instead on functional brain activity in reward processing systems during anticipation of monetary rewards at age 16. The vast majority of studies investigating the effects of social context on the brain have focused on brain structure. However, since a precise understanding of the relations between brain structure and function in the developing brain is still emerging, it is also important to examine how variations in the social context are associated with functional activity in the brain, especially in regions of the brain that support social and emotional processes. Casement et al. show that, in a community sample of girls, adolescent-reported parental warmth in early adolescence is associated with activity in a reward processing circuit that includes the medial prefrontal cortex (mPFC), striatum and amygdala. Activity in the striatum and mPFC further accounts for the relationship between maternal warmth and depressive symptoms.

Tan et al. also investigate the influence of parenting on functional brain activity during adolescence, but extend

this work by focusing on neural response to social rather than monetary reward. This is important because social rewards, such as inclusion and acceptance from peers, are believed to be of high motivational and affective salience during adolescence (Nelson et al., 2005). Consistent with a growing trend in developmental social and affective neuroscience research (e.g. Davey et al., 2010; Gunther Moor et al., 2010; Guyer et al., 2008; Masten et al., 2009; Silk et al., 2012b), Tan et al. investigate the neural response to simulated peer acceptance and rejection from fictitious “virtual” peers during neuroimaging. Findings from the Tan et al. paper indicate that higher levels of maternal negative affect during an observational task designed to elicit parental support are associated with a blunted response to peer acceptance across a network of regions involved in responding to reward and other emotional stimuli, such as the nucleus accumbens, amygdala, anterior insula, and subgenual anterior cingulate cortex. These findings suggest that negative mother-adolescent interactions have the potential to dampen responsiveness to social rewards, even in interactions with other social partners, such as peers. This process could be particularly detrimental during adolescence given the importance of rewarding social interactions with peers during this period of development (Steinberg & Morris, 2001).

It is also interesting to note that findings in the Tan et al. study emerged for negative parenting in a typically positive context, while findings in the Whittle et al. study emerged for positive parenting in a typically negative context. Both studies found few results when investigating context-consistent parenting (i.e. positive parenting during a support task or negative parenting during a conflict task). Other studies have shown that levels of negative parenting behavior in a typically positive context are often important for predicting outcomes, such as depressive symptoms (McMakin et al., 2011; Whittle et al., 2009). Collectively, these findings suggest that the display of “context-inconsistent” emotions during interpersonal interactions may be particularly impactful for neurobehavioral development.

The Whittle et al., Casement et al., and Tan et al. studies are noteworthy for focusing on the influence of parenting during adolescent development. Very little research has investigated the effects of parenting during adolescence on neural structure and function, perhaps because of the assumed increasing importance of the peer social context of adolescence on youth. However, adolescents continue to rely on support from their parents in navigating the social and emotional challenges of adolescence, and parenting during adolescence is predictive of social adjustment and mental health (Schwartz et al., 2012; Steinberg & Silk, 2002; Williams & Steinberg, 2011). The plasticity of neural circuits during the important developmental transition period of adolescence suggests that there is a need for additional research on how parental caregiving influences contribute to brain structure and function during this period.

Although these studies highlight the continued importance of parent-adolescent relationships during adolescence, it is clear that peer relationships have a special salience during adolescence. Jankowski, Moore,

**Merchant, Kahn, & Pfeifer** use a novel self-evaluation paradigm to examine adolescents' and adults' brain activity when reflecting upon how they believed they would be evaluated by a close friend. This fMRI paradigm, which requires participants to reflect upon what they think others would say about them, represents another method for infusing a more ecologically valid social dimension into developmental cognitive neuroscience research. Findings show that perceived evaluations by peers uniquely activate the ventral striatum in comparison to a control condition in adolescents relative to adults. This finding suggests that adolescents may be uniquely sensitive to social evaluation, which is known to play a key role in identity development during adolescence (**Pfeifer et al., 2007, 2009**). **Jankowski et al.** also show that ventral striatal activation to perceived evaluation from a peer increases as a function of age and pubertal development, suggesting that enhanced sensitivity to peer evaluation is a normative developmental process. This is consistent with a recent study showing that pubertal development is associated with increased ventral striatal response to simulated peer rejection in adolescents (**Silk et al., 2014**).

### 3. Theme 2: Role of reward and threat circuitry (and their interactions) in developmental psychopathology

All of the papers discussed in the previous section investigated brain structure and function within reward processing circuits including the ventral striatum, mPFC, and OFC (see review by **McClure et al., 2004**). This is consistent with a growing recognition of the importance of reward function in the development of psychopathology (**Forbes & Dahl, 2005; Pizzagalli, 2014; Pujara & Koenigs, 2014**). Research conducted by Forbes and colleagues (**Forbes et al., 2006, 2009**) has highlighted the role of reduced ventral striatal response to monetary reward in adolescent depression. **Olino et al.** extend this work by showing that a sample of non-depressed adolescents at high familial risk for depression show a similar pattern of reduced striatal response during anticipation of monetary reward. This is consistent with two recent studies demonstrating altered striatal functioning in response to positive stimuli in adolescents at high risk for depression (**Gotlib et al., 2010; Monk et al., 2008**) and a growing body of research suggesting that reduced striatal response to reward may be an endophenotype for depression risk (**Hasler et al., 2004**).

While the evidence for altered reward functioning in depression is strong, far less is understood about the functioning of reward systems in anxiety. Although the influential "tripartite model" posits that reduced positive affect is specific to depression rather than anxiety (**Clark & Watson, 1991**), results have been mixed in studies of children and adolescents with anxiety disorders and symptoms, who often show reduced positive affect relative to non-anxious youth (**Anderson et al., 2010; Chorpita et al., 2000; Jacques & Mash, 2004**). **Silk et al., 2012a** proposed that alterations in reward processing in a subset of anxious youth may help to explain the common trajectory from anxiety in early and middle childhood to depression later

in adolescence. In this special section, **Caouette and Guyer** review a growing neuroimaging literature on the role that reward and fear-processing circuits play in risk for social anxiety disorder (SAD), a common form of anxiety during adolescence. This review points out that although initial studies of the neural correlates of SAD pointed to alterations in the amygdala and ventral prefrontal cortex (areas prominently involved in processing and regulating response to threat), recent neuroimaging studies in adolescents with and at risk for anxiety disorders reveal altered functioning in reward-processing structures in the basal ganglia. **Caouette and Guyer** present a conceptual model which proposes a key role for approach-avoidance conflict, particularly in adolescent-normative social experiences, in the development of SAD during this period. They also highlight the potential for research on reward processing to reveal novel ways to improve treatments for social anxiety in adolescence.

**Ernst et al.** also investigate risk/reward trade-offs in adolescent anxiety, but focus on the phenomenon of loss aversion, which has received little attention in the developmental literature. They use a computerized betting task to demonstrate that loss aversion is present in adolescents and is modulated by the 5HTT gene, which has been associated with impulsivity. Interestingly, they identify a subset of anxious adolescents that are high 5HTT-expressers who are actually low in loss aversion and high in impulsivity. This work may point toward identification of those anxious adolescents who are most likely to develop comorbid externalizing disorders.

Both the **Caouette and Guyer** and **Ernst et al.** papers introduce the possibility that reward and threat systems may interact during adolescence in ways that can lead to anxiety in some youth as well as externalizing behaviors in others. Recently, **Spear (2011)** raised the intriguing possibility that adolescence may be characterized by high-levels of "cross-reactivity" between areas involved in processing reward and threat stimuli. Consistent with this idea, **Spielberg, Forbes, Olino, and Dahl** present a conceptual model in this special section suggesting that hormonal changes associated with pubertal development, particularly the rise in testosterone, may be related to a greater capacity to experience fearful situations as simultaneously threatening and rewarding. They present preliminary support for this model from a longitudinal study of pubertal development and discuss future steps needed to fully evaluate the model. Because of the novelty of these ideas we invited commentary from other researchers studying adolescent brain development (**Helfinstein & Casey**) to discuss the links between this model and current thinking in the field.

### 4. Theme 3: Emotion–cognition interactions

Although the focus of this special issue is on social and affective development, these domains should not be thought of as independent from cognition. Research in adults has highlighted the complex interplay between emotion and cognition and suggests that in many cases classifying brain regions as affective or cognitive is untenable (e.g., **Pessoa, 2008**). Studies examining emotion

cognition interactions across development are just appearing in the brain imaging literature. For example, [Perlman and colleagues](#) developed a novel task to examine attention-emotion interactions by including a task-irrelevant emotional distracter during an oddball task. They find an effect of emotional valence in orbitofrontal cortex that moderately increases with age and is related to individual differences in emotion regulation. These findings could provide an important normative baseline for studies of populations at-risk for difficulties with emotion regulation. In fact, [Thomas et al.](#), provide evidence of atypical attention-emotion interactions in youth with severe mood dysregulation (SMD) and bipolar disorder (BD). Specifically, they found that regions within occipital cortex were recruited more when SMD and BD participants were *unaware* of an emotional face as compared to when aware (through a masked priming study). The reverse effect was found in healthy control participants. Thus, atypical emotion processing in participants with these mood disorders persists even in contexts of reduced attention. Finally, the importance of attention to cognition-emotion interactions in understanding atypical development is nicely highlighted by [Vander Wyk and colleagues](#) by demonstrating that previously reported differences between autism and control groups during an emotion processing task (e.g., [Schulte-Rüther et al., 2011](#); [Silani et al., 2008](#)) may have been influenced by the cognitive demands of the task. When cognitive demands were minimized, no differences were found between groups on emotion processing tasks ([Vander Wyk et al.](#)). While a within-group comparison is warranted, these findings have important implications for understanding of the “core” impairments in autism. In sum, these studies add to a small growing literature on the typical development of attention-emotion interactions and their importance in our understanding of emotional processing in psychopathology.

#### **5. Theme 4: Charting the early typical and atypical development of socio-affective processing.**

Infancy and early childhood are periods marked by exuberant changes in brain development and significant advances in social and emotional development (e.g., [Courchesne et al., 2000](#); [Fox & Calkins, 2003](#); [Johnson et al., 2005](#); [Wellman, 2011](#)). The relation between these changes in the brain and behavior, and the role of experience in driving these changes remains unspecified. While most of the papers in this special issue focus on adolescence, several papers highlight the striking paucity of normative data on brain-behavior relations supporting socio-emotional development during infancy and early childhood ([Luyster et al.](#); [Nelson et al.](#); [Rice et al.](#)). The absence of normative data presents a major barrier to accurately identifying and interpreting neural markers of risk for early emerging disorders characterized by social difficulties, such as autism spectrum disorder. Several papers in the current issue aim to fill in these gaps by charting the developmental trajectory of ERP components across 6–36 months of age ([Luyster et al.](#)), by examining the role of early experience on neural sensitivity to social

stimuli ([Nelson et al.](#)), and by examining the role of the amygdala in children’s developing social-cognitive abilities ([Rice et al.](#)). These papers additionally highlight important ways in which understanding normative development is critical to interpretations of atypical development.

One of the important messages from the studies in this special section is that the relations between brain structure, brain function, and behavior are nonlinear and can change throughout development ([Luyster et al.](#); [Rice et al.](#); [Whittle et al.](#)). For example, [Rice et al.](#), and [Whittle et al.](#), both demonstrate a relation between amygdala size and social behavior. However, whereas [Rice et al.](#), demonstrate a positive relation between amygdala volume and performance on social tasks of face-based mental state inference in early childhood, [Whittle et al.](#), demonstrate a negative relation between amygdala growth in mid-adolescence and positive parenting behavior. This seemingly reversed pattern is partly due to the fact that amygdala growth is nonlinear ([Uematsu et al., 2012](#)). Thus, larger amygdala in early childhood and attenuated amygdala growth in mid-adolescence may both indicate an amygdala trajectory ahead of the normative curve for social-emotional development. Another intriguing possibility is that the function of the amygdala in social behavior may shift depending on the developmental stage. Hints for a developmental shift in the functional role of the amygdala come from animal and human studies (reviewed in [Adolph, 2010](#); [Rice et al.](#)). This research highlights the need for more longitudinal studies from early childhood through adolescence that carefully characterize how social experience relates to amygdala growth rates and how those growth rates in turn relate to developing social and emotional abilities throughout development. In a second example of nonlinear change, [Luyster and colleagues](#) chart the development of four event-related potentials (ERPs) relevant to face processing (P1, N290, P400, and Nc) in a longitudinal sample of infants from 6 to 36 months of age who are at high and low risk for developing autism spectrum disorder. They found nonlinear changes in the amplitude of these face-sensitive components, including increasing amplitude of the Nc and P400 components in the first two years of life but decreasing amplitude in the third year of life. Previous studies have also revealed a shift in the sensitivity of face-relevant components to familiar vs. unfamiliar stimuli between infancy and childhood ([Carver et al., 2003](#); [Moulson et al., 2009](#)).

Maturation and experiential factors necessarily play an interactive role in driving these trajectories but the extent to which each contributes to these patterns remains an open question. *Theme 1* above addressed the role of social contexts on social and affective neural circuits during adolescence but infancy is also period in which experience can have a dramatic effect on shaping socio-emotional circuits. For example, infants begin life able to discriminate faces within their own and other species. With age and experience, this ability narrows and refines to individuals within one’s own species. However, analogous to findings of speech perception ([Kuhl et al., 2003](#); [Werker & Yeung, 2005](#)), if infants are given early experience with faces of other species the period of time during which they can discriminate nonnative species faces is lengthened ([Pascual](#)

et al., 2005). Similarly, infants are better able to discriminate faces within the racial (Bar-Haim et al., 2006) and gender (Quinn et al., 2002) categories with which they have the most experience. Less data have addressed how typical variations in early experience shape brain responses to social stimuli in the first year of life. In the current issue, Nelson and colleagues examine the role of experience with female faces on infants' developing neural sensitivity to male and female faces at 7 months. They found that for "female experts" (i.e. infants with disproportionate experience with female faces), female faces elicited a greater N290 response than did male faces. Thus, social experience with faces drives sensitivity of face-sensitive components in early infancy.

Taking the role of social experience into consideration is particularly important when trying to identify neural signatures of infants with autism. Behavioral studies of infants at-risk for autism reveal differences in the extent of social attention beginning in the first years of life (e.g., Jones & Klin, 2013; Pierce et al., 2011). However, an ERP study in the current issue by Luyster et al., finds no differences in the ERP response to faces in infants at-risk for autism. Instead, differences emerge near the end of the second year of life. One possibility to reconcile these findings is that some candidate neural "markers" of autism may reflect a history of reduced social experience with faces rather than a driving causal influence of atypical social development (cf. Pelphrey et al., 2011, regarding functional connectivity). This is not to suggest that all neural signatures reflect consequences rather than causes, rather these findings emphasize the need for more multimodal, longitudinal studies of both normative and atypical development of social and emotional circuits and their relation to experience.

## 6. Concluding comments

This set of papers highlights advances in the attempt to characterize the role of social and emotional experience on structural and functional brain development (and the reverse) during infancy, early childhood, and adolescence. One of the most significant challenges in addressing questions such as these is the need to develop experimental paradigms that capture developmentally salient socio-affective experiences without compromising experimental design. Several of the papers in this special section present approaches that enhance the ecological validity and/or socio-affective salience of experimental stimuli, such as the use of simulated virtual peer interaction paradigms (Tan et al.), use of pictorial stimuli depicting familiar people, such as infants' own mothers (Luyster et al.), use of perspective manipulations to encourage youth to consider how they are evaluated by familiar people, such as peers (Jankowski et al.), and use of priming approaches (Nelson et al., Thomas et al.). These authors have moved beyond the use of static simple stimuli to the presentation of dynamic complex social events. Such work pushes us to think about the multiple cognitive processes and affective responses that are involved in social interaction. They force us to acknowledge that "real life" interaction is complex and that we must deal with that complexity in the

interpretation of brain responses when presenting stimuli that model such interactions. The studies in the current section raise three questions for further consideration. First, are we at a point in our science where we have the paradigms and experimental control to model social interaction and understand complex brain function? The papers in this section suggest that we are getting there. Second, can we guard in our science against reverse inference often found in imaging studies? Too often activation in brain areas is interpreted as signifying changes in cognition when the functional significance of those brain areas is still in debate. The current papers in this section do a commendable job in the care with which they frame their findings avoiding this pitfall. And third, can we utilize brain imaging studies to understand the etiology of mental disorders? The current studies highlight the complexities of this task but provide an admirable base from which important aspects of developmental change as a function of context can be used to understand the brain bases of mental disorders. There is much work to be done, but the work in this section highlights progress and promise.

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