



Neurodevelopmental changes across adolescence in viewing and labeling dynamic peer emotions



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ABSTRACT

Adolescence is a sensitive period of social-affective development, characterized by biological, neurological, and social changes. The field currently conceptualizes these changes in terms of an imbalance between systems supporting reactivity and regulation, specifically nonlinear changes in reactivity networks and linear changes in regulatory networks. Previous research suggests that the labeling or reappraisal of emotion increases activity in lateral prefrontal cortex (LPFC), and decreases activity in amygdala relative to passive viewing of affective stimuli. However, past work in this area has relied heavily on paradigms using static, adult faces, as well as explicit regulation. In the current study, we assessed cross-sectional trends in neural responses to viewing and labeling dynamic peer emotional expressions in adolescent girls 10–23 years old. Our dynamic adolescent stimuli set reliably and robustly recruited key brain regions involved in emotion reactivity (medial orbital frontal cortex/ventral medial prefrontal cortex; MOFC/vMPFC, bilateral amygdala) and regulation (bilateral dorsal and ventral LPFC). However, contrary to the age-trends predicted by the dominant models in studies of risk/reward, the LPFC showed a nonlinear age trend across adolescence to labeling dynamic peer faces, whereas the MOFC/vMPFC showed a linear decrease with age to viewing dynamic peer faces. There were no significant age trends observed in the amygdala.

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1. Introduction

Adolescence is often perceived to be a sensitive period for social and emotional development. Indeed, compared to children, adolescents spend more time interacting with peers, and exhibit greater concern with social status, friendships, and romantic relationships (Brown and Larson, 2009; Furman et al., 2009; Suleiman and Harden, 2016). The behaviors, beliefs, or mere presence of peers have also been shown to influence adolescents at various behavioral and neurobiological levels (Doom et al., 2016; Peake et al., 2013; Shulman et al., 2016). In addition to this period of heightened sensitivity to peers, adolescents may display greater emotional variability than adults (Larson et al., 2014), heightened intensity of emotion, regardless of valence (Silk et al., 2009), and particular difficulty regulating emotions elicited by social stimuli (versus nonsocial; Silvers et al., 2012). Taken together, these concurrent changes during adolescence highlight a significant need to better

understand the developmental trajectories of affective processing elicited by peer faces.

For the past decade and a half, there has been growing research interest in understanding how these social and affective changes are related to neural development, given that adolescence is also a period of remarkable neural plasticity (Kadosh et al., 2013; Zelazo and Carlson, 2012). Indeed, it is now widely accepted that key regions and networks involved in social cognition, emotional reactivity, and emotion regulation all undergo significant functional development during adolescence (Casey et al., 2008; Pfeifer and Blakemore, 2012; Somerville et al., 2011a). However, the field's existing models of socio-affective neurodevelopment in adolescence (Nelson et al., 2016, 2005) largely describe which brain regions are implicated in these tasks, rather than more precisely proposing when and how the functioning in these regions change (Pfeifer and Allen, 2016). In comparison, dual systems and imbalance models have been used extensively to explain sensitive periods in adolescent risk behavior, and propose age-based trajectories for sensitivity to rewards and regulatory capacities, as well as describe the relationships between these trajectories (Blakemore and Robbins, 2012; Casey et al., 2016; Shulman et al., 2016). These models have sometimes been applied to under-

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standing affective changes in adolescence (Crone and Dahl, 2012; Pfeifer and Allen, 2012; Somerville et al., 2011a), but have been less extensively tested in this domain. Therefore, one aim of this study was to explore whether brain functioning elicited by socio-affective stimuli reveals a similar sensitive period of imbalance in our cross-sectional sample (following Giuliani and Pfeifer, 2015; Hare et al., 2008; Somerville et al., 2013); such that neural indices of socio-affective reactivity would exhibit non-linear developmental trajectories, with activity peaking by middle adolescence, and that regulation-related responses would display roughly linear patterns of change across the duration of adolescence. In order to acknowledge the importance of peers for affective and regulatory neurodevelopment in adolescence, the current study used a novel set of dynamic adolescent facial expressions.

1.1. Brain regions and networks implicated in the regulation of emotion processing

The adult neuroimaging literature provides a solid roadmap for beginning to understand adolescent affective reactivity and regulation. Passive viewing of facial affective stimuli by adults is associated with increased activity in key neural regions such as the amygdala (Fitzgerald et al., 2006; Fusar-Poli et al., 2009; Sabatinelli et al., 2011), medial orbitofrontal cortex (MOFC; (Liang et al., 2009; Monk et al., 2003; Ochsner et al., 2002) and ventral medial prefrontal cortex (vmPFC; (Ebner et al., 2012). When further cognitive processes are layered onto viewing affective stimuli, such as reappraisal or labeling of the emotional content of the stimulus, additional regions are recruited by adults to modulate the response to the affective stimuli, particularly the lateral prefrontal cortex (LPFC; (Buhle et al., 2014; Lieberman et al., 2007; Wager et al., 2008).

Across adolescence, these key regions from networks supporting reactivity and regulation show varied nonlinear and linear age-related patterns of functional activity, respectively, to affective stimuli. For example, some studies show an adolescent peak in amygdala activity to affective facial stimuli (Guyer et al., 2008; Hare et al., 2008; Monk et al., 2003), although others have not observed this non-linear pattern (Gee et al., 2012; Pfeifer et al., 2011); a similar finding with non-facial affective stimuli has been observed (Vink et al., 2014). Meanwhile, functional recruitment of the LPFC often shows a linear pattern across adolescence, although the direction of change can vary. In affect regulation tasks using facial stimuli, increases have been observed (Gee et al., 2012), while regulation of non-facial affect has shown both increases (McRae et al., 2012) and decreases (Vink et al., 2014). In broader assessments of LPFC engagement across a variety of regulatory and executive function tasks, findings have likewise been mixed (for review, see Crone and Dahl, 2012). Finally, contrary to adult studies using affective paradigms, adolescent studies do not show the same MOFC activity to facial affective stimuli; however, MOFC is frequently observed in studies of adolescent reward sensitivity and non-facial emotion processing (Galvan et al., 2006; Rothkirch et al., 2012; Vink et al., 2014). One possibility for the absence of MOFC activity in adolescent studies of facial affective processing is that adult faces are less rewarding or motivationally salient to adolescents. This suggests that aspects of task design including stimuli selection may critically influence the degree or kind of neurodevelopmental changes in cortical and subcortical recruitment that are observed in adolescence, and thus our inferences about whether adolescence is a sensitive period with respect to particular processes (Blakemore and Robbins, 2012; Crone and Dahl, 2012; Pfeifer and Allen, 2012).

1.2. Developmentally salient stimuli

As adolescents increasingly build autonomy from their parents, more time is spent with peers and a greater value is placed on peer and romantic relationships (Brown and Larson, 2009; Furman et al., 2009; Suleiman and Harden, 2016), making the ability to identify peers' emotions particularly important for successful social functioning. However, prior research examining changes in reactivity and regulatory regions across adolescence has been limited by primarily relying on adult facial expressions to probe emotion processing (Ekman faces; Ekman and Friesen, 1976; Tottenham et al., 2009), or other adult-oriented affective stimuli, such as the International Affective Picture System (IAPS; Britton et al., 2006; Vink et al., 2014), with a few notable exceptions (child stimuli sets: CAFE; LoBue and Thrasher, 2015; NIMH-chEFS; Egger et al., 2011).

There is evidence to suggest that child and adult faces may elicit different patterns of brain activity (Leibenluft et al., 2004). In fact, studies that have directly compared peer and adult facial expressions found both children and adolescents recruit largely similar brain regions to peer and adult faces, but exhibit increased amygdala activity to positive peer faces and angry adult faces, which may represent an age-appropriate response to the stimuli (8–16 year olds: Marusak et al., 2013; 5–6 year olds: Hoehl et al., 2010). In addition, when adolescents were asked to rate and receive feedback from peers (based on viewing peer faces), 8–17 year old females showed increased nucleus accumbens activity across age (Guyer et al., 2009). These data suggest that peer faces, particularly in adolescence, may modulate the affective response elicited and/or the observed neural correlates. Despite the importance of peers during this sensitive period of facial affective processing, however, there is still a relative dearth of studies examining adolescent development of neural responses elicited by peer facial expressions or other adolescent-oriented affective stimuli.

Additionally, the stimuli used in the extant literature are largely static images, and are of relatively more extreme expressions or situations than the emotional content individuals experience on a daily basis. Neuroimaging studies in adults suggest that relative to static emotional expressions, neural responses to dynamic emotional expressions are more robust (Pitcher et al., 2011; Sato et al., 2004). Taken together, this research suggests that dynamic emotional expressions made by peers, rather than adults, may be particularly salient to adolescents and an important option to pursue in the attempt to enhance the ecological validity of fMRI tasks.

1.3. Implicit regulation

In addition to the use of adult, static faces, previous paradigms used to assess adolescent brain function associated with emotion processing have ranged from implicit, non-instructed passive viewing (Pfeifer et al., 2011) to explicit, instructed regulation or reappraisal tasks (Crowley et al., 2014; McRae et al., 2012; Pitskel et al., 2014; Silvers et al., 2012), with some paradigms falling in between, such as behavioral inhibition tasks that utilize affective stimuli (Somerville et al., 2011b). The literature on emotion regulation in adolescence has predominantly focused on explicit (e.g., instructed to regulate) or partially explicit emotion regulation strategies (e.g., instructed to inhibit response, such as go/no-go tasks; Mauss et al., 2007). However, implicit emotion regulation, or regulation without intention, awareness, or insight, is an equally important strategy that is not mutually exclusive from explicit emotion regulation (Gyurak et al., 2011). Research suggests that these strategies recruit the same key reactivity and regulatory brain regions as explicit emotion regulation paradigms in adults (Gyurak et al., 2011; Lieberman et al., 2007), but may additionally serve as a more ecologically valid assessment of real-world tendencies to

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