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Review article

Social connectedness, mental health and the adolescent brain

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ABSTRACT

Social relationships promote health and wellbeing. Brain regions regulating social behavior continue to develop throughout adolescence, as teens learn to navigate their social environment with increasing sophistication. Adolescence is also a time of increased risk for the development of psychiatric disorders, many of which are characteristically associated with social dysfunction. In this review, we consider the links between adolescent brain development and the broader social environment. We examine evidence that individual differences in social ability, partly determined by genetic influences on brain structure and function, impact the quality and quantity of social ties during adolescence and that, conversely, the structure of one's social network exerts complex yet profound influences on individual behavior and mental health. In this way, the brain and social environment sculpt each other throughout the teenage years to influence one's social standing amongst peers. Reciprocal interactions between brain maturation and the social environment at this critical developmental stage may augment risk or promote resilience for mental illness and other health outcomes.

Adolescence is a period of pronounced physical, emotional and social transformation (Blakemore, 2012; Casey et al., 2008). A major aspect of this transformation is a growing investment in social relationships outside the primary family unit, which form a critical foundation for the development of an independent sense of identity (Larson and Richards, 1991; Larson et al., 1996). This transition requires adolescents to engage in more complex social interactions, as teens start to model their own behavior on the actions and influences of peers, and to learn how their own actions affect others (Burnett and Blakemore, 2009). These changes in social engagement coincide with a period of marked brain development, characterized by the refinement of synaptic connectivity and the maturation of long-range axonal pathways that support the functional integration of wide-spread neural systems, including those involved in the processing of social information (Baker et al., 2015; Huttenlocher, 1990; for a review, see Paus, 2005; Webb et al., 2001). The concurrent changes in the social environment and brain function that occur during adolescence suggest that the two may shape each other as individuals develop from children into mature adults.

People do not develop in isolation; they are embedded within a complex web of social relations, where even subtle and indirect influences can impact one's well-being (Aral and Walker, 2012; Christakis and Fowler, 2013; Kadushin, 2011; Rosenquist et al., 2011). Studies of extended social networks have shown that the structure of adolescents' friendships can have strong impacts on health and development (Ali and Dwyer, 2010; Haas and Schaefer, 2014; Hatzenbuehler et al., 2012; Hill et al., 2015; Mednick et al., 2010). However, it is largely unknown how the social environment affects adolescent brain maturation and, in turn, how neurodevelopmental processes influence teenage social behavior. Adolescence is a period of increased vulnerability to the onset of mental illness (Merikangas et al., 2010; Paus et al., 2008) and these disorders may both cause, and be a consequence of, social dysfunction and isolation (for reviews, see Fett et al., 2015; Meyer-Lindenberg and Tost, 2012). Therefore, understanding the relationship between neurobiological and social development during adolescence may shed light on developmental pathways associated with risk or resilience for psychopathology.

Here, we consider the evolution of social behavior through adolescence, and its implications for mental health, from the perspectives of neurobiology and social network science. We review the ways in which adolescent friendships impact upon the brain and mental health, and examine the potential of social interventions for improving health outcomes during this critical stage. Finally, we evaluate the implications of online relationships and social behavior, and discuss the ways

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in which new technologies can be harnessed to promote social connectedness and improve mental well being.

1. The social brain in adolescence

The human brain undergoes a protracted period of development that extends into the third decade of life (Webb et al., 2001). Adolescence is a period of prominent structural and functional brain maturation, characterized by a gradual and global decrease in cortical grey matter volume, in concert with a progressive increase in white matter volume and density (Giedd and Rapoport, 2010; Paus, 2005). These changes are consistent with ongoing myelination of long-range axonal pathways and intra-cortical connections (Alexander-Bloch et al., 2013; Baker et al., 2015; Whitaker et al., 2016), but may also be related to continued synaptic pruning in specific neural systems, including those involved with social processing (Blakemore, 2012; Casey et al., 2008; Huttenlocher, 1979).

Social information processing depends on many different abilities in order to perceive, interpret and understand the behavior and mental states of others. It is thought to arise from interactions between several functionally specialized, yet inter-related, neural systems. In this review, we will primarily focus on the affective, cognitive-regulatory and mentalizing systems as they relate to emerging social behavior in adolescence (Fig. 1). The affective system includes the amygdala, striatum, nucleus accumbens (NAcc), hypothalamus, ventrolateral prefrontal cortex (vlPFC), ventral anterior cingulate and the anterior insula, and assigns emotional and social significance to perceptual stimuli in support of approach and avoidance responses (Guyer et al., 2016; Nelson et al., 2005). The cognitive-regulatory system comprises areas of orbitofrontal, dorsomedial and ventral pre-frontal cortex (Nelson et al., 2005). This network rapidly and flexibly evaluates context and meaning from social stimuli, regulates appropriate emotional reactions and inhibits impulsive behavior (Nelson et al., 2005). The final system mediates mentalizing—the ability to assign mental states to the self and others (also known as Theory of Mind, or ToM)—and is based around a core network of regions focused on the medial pre-frontal cortex (mPFC), temporoparietal junction (TPJ) and superior temporal sulcus (STS) (Frith and Frith, 2003; Schurz et al., 2014). Each of these social brain systems is subject to ongoing structural and functional development throughout adolescence, in parallel with changes in social behavior (Blakemore, 2008; Blakemore and Mills, 2014).

According to one prominent theory, there is a developmental mismatch between the early maturation of key subcortical structures comprising the affective system, and the more protracted development of pre-frontal regions involved in the cognitive and mentalizing systems, which reach full maturity in early adulthood (Casey et al., 2008; Somerville et al., 2010; Steinberg, 2008). The developmental mismatch hypothesis posits that deficient prefrontal regulation of reward and affect processing contributes to the high emotional salience assigned to peer influence during adolescence, as well as a number of behaviors that typically characterize adolescence, such as increased risk-taking and sub-optimal decision making (Guyer et al., 2009; Jones et al., 2014; Peake et al., 2013). Consistent with this view, numerous neuroimaging studies have reported increased activation of the affective system in adolescents compared to adults during tasks assessing risk-taking and reward processing (Braams et al., 2015; Ernst et al., 2005; Galvan et al., 2006; Somerville et al., 2011; Van Leijenhorst et al., 2010), lending support to the role of increased subcortical signaling in social decision making during adolescence. One large functional MRI study comprising 269 participants, aged 8–25 years, found linear age-related increases in the functional coupling of pre-frontal and subcortical structures (Van Duijvenvoorde et al., 2015). This finding would be consistent with enhanced top-down modulation of frontal over subcortical areas, although the directionality of functional coupling was not resolved in this study.

There is also some evidence to suggest that these functional changes are accompanied by alterations in brain structure. One longitudinal study focusing on the amygdala, the NAcc and regions of interest in the pre-frontal cortex (PFC), found that the amygdala matures relatively earlier than the PFC, consistent with a developmental mismatch between these two regions, whereas the NAcc continues to develop into early adulthood (Mills et al., 2014a). Amygdala grey matter volume (GMV) increased gradually by 7% in the period from childhood (7–11 years) to adolescence (12–17 years), but stabilized from approximately 16 years, whereas NAcc GMV decreased steadily by 7% from childhood to adulthood (18–26). In contrast, GMV of the PFC decreases by 17% between adolescence and adulthood (Mills et al., 2014a). Consistent with these findings, other work has shown that structural development of subcortical regions within the affective system is

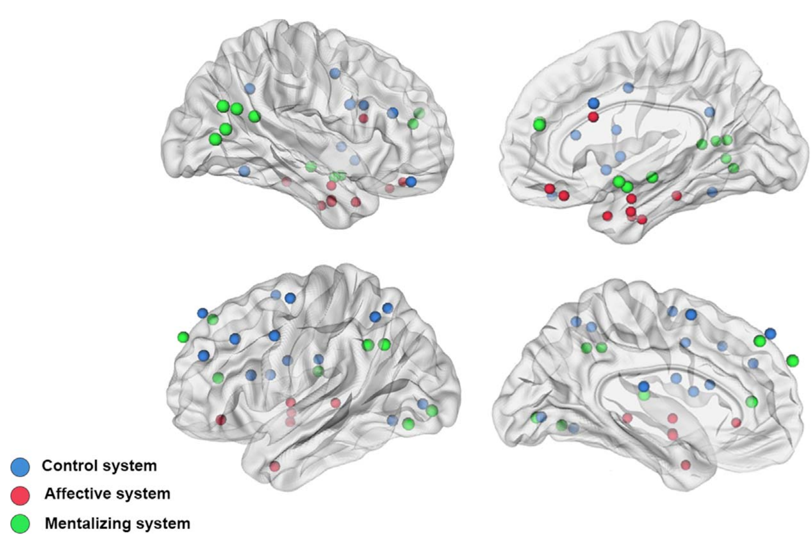

Fig. 1. Brain systems involved in social information processing. The affective system comprises the amygdala, striatum, hypothalamus, ventral anterior cingulate, ventrolateral pre-frontal cortex and anterior insula. The control system includes dorsal, ventral and orbital regions of prefrontal cortex, the superior temporal sulcus and superior parietal cortex. The mentalizing system includes the medial prefrontal cortex, fusiform gyrus, anterior cingulate and cortex adjacent to the posterior superior temporal sulcus. This figure shows key cortical regions involved in each system. Coordinates for the affective system were obtained from the functional connectivity analysis of (Bickart et al., 2012). Coordinates for the control and mentalizing system were obtained from the meta-analyses of (Niendam et al., 2012) and (Schurz et al., 2014), respectively. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.