

A framework for integrating neural development and social networks in adolescence

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ABSTRACT

Adolescence is a developmental period characterized by increasingly complex and influential peer contexts. Concurrently, developmental changes in neural circuits, particularly those related to social cognition, affective salience, and cognitive control, contribute to individuals' social interactions and behaviors. However, while adolescents' behaviors and overall outcomes are influenced by the entirety of their social environments, insights from developmental and social neuroscience often come from studies of individual relationships or specific social actors. By capturing information about both adolescents' individual relations and their larger social contexts, social network analysis offers a powerful opportunity to enhance our understanding of how social factors interact with adolescent development. In this review, we highlight the relevant features of adolescent social and neural development that should be considered when integrating social network analysis and neuroimaging methods. We focus on broad themes of adolescent development, including identity formation, peer sensitivity, and the pursuit of social goals, that serve as potential mechanisms for the relations between neural processes and social network features. With these factors in mind, we review the current research and propose future applications of these methods and theories.

Adolescence is a developmental period in which changing peer contexts play an increasing role in shaping individuals' social, emotional, and cognitive development. During a time in which biological and cultural factors heighten the salience of peers' behaviors and norms, adolescents must navigate increasingly complex relationships and social environments. Thus, individual friendships and larger social network structures play a profound role in influencing adolescent behaviors and outcomes. While neuroimaging research to date largely focuses on relationships between individuals (e.g., friendship pairs), it is important to consider how individuals perceive and navigate their larger social environments. Social network analysis (SNA) provides powerful opportunities to capture information about both individual relationships and characteristics of larger social groups. While SNA has been integrated with cognitive (reviewed in Smith et al., 2020) and social (reviewed in Baek et al., 2021) neuroscience research, less research has focused on this integration in developmental neuroscience, particularly during adolescence when changes in neural development and social structures are associated with behavioral outcomes. Thus, the purpose of this review is to synthesize research on the relations between

neurodevelopment, social groups, and behavioral outcomes, and to identify the developmental factors that should be considered when applying this work to adolescents.

1. A framework for integrating neuroimaging and social network data in adolescence

Researching adolescent social development is a complex and multifaceted undertaking. Even alone, neuroimaging, social network, and behavioral data each present unique challenges, and applying them all toward an understanding of adolescent development and outcomes relies on numerous theories and bodies of research. Moreover, understanding adolescence not as a single monolithic period, but rather an unfolding developmental process, presents the challenge of capturing mechanisms as they progress across varying time windows. Nonetheless, each mode of data offers unique insights into adolescent development. Neuroimaging allows researchers to probe the neural systems and mechanisms that support social processes, and evaluate how individual differences in neural function and connectivity relate to various

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behaviors and outcomes. In contrast, social network data, and particularly longitudinal social networks, can capture myriad features of adolescents' lived social experiences, including features such as friendships, status, connectedness, peer influence, and more. Other psychological methods, such as surveys, cognitive experiments, or observations, can be integrated with neuroimaging and social network data in many ways, such as probing mediating mechanisms or understanding positive and negative trajectories of outcomes. Given the multidimensional nature of these types of data, as well as the difficulty in obtaining them, relatively little research has integrated both neuroimaging and social network analysis, and nearly no studies have incorporated a developmental framework. However, social and developmental neuroscientists are increasingly recognizing the need to capture social information outside of individual relations, and turning to social network analysis to better understand social processes (Baek et al., 2021).

Here, we aim to introduce a broad framework (Fig. 1) that will orient social and developmental neuroscientists, particularly those interested in adolescence, toward promising mechanisms and pathways that may underlie the relations between neurodevelopment and peer network features. Broadly, we posit that neural regions² involved in social cognition, affective-salience, and cognitive control, interact with one another to scaffold psychosocial processes (which can also interact with one another) that influence both how adolescents orient toward their peer networks, and how they interpret social feedback and their own positions within these networks.

Briefly, we will review social network analysis (SNA), and how it can capture salient features of adolescents' peer networks. Subsequently, we will introduce theories of adolescent development related to identity, sensitivity to peers, and social goals that form the basis of our framework, noting ways in which SNA can expand our knowledge of these theories and constructs. Then, we will review studies that integrate SNA and neuroimaging methods in adults and adolescents – highlighting the features of adolescence that should be considered when interpreting and continuing those lines of research. Lastly, we will offer future themes and directions that should be explored when combining SNA and neuroimaging methods in adolescence.

2. Social network analysis: Studying adolescents' peer networks

As individuals move from childhood to adolescence, friendships and peer contexts become more complex and more impactful. On the friendship level, individual relationships become more intimate, characterized by factors such as increased disclosure and greater expectations of reciprocity (Brown, 2004; Brown and Larson, 2009). Concurrently, dynamic social networks, particularly in the school context, also impact adolescents' social lives (Cotterell, 2013). Factors such as school transitions, increased opportunities to engage in social and extracurricular activities, and greater access to peers via digital and social media, all afford adolescents the opportunities to form new friendships and identify with different social groups (Brown and Larson, 2009; Lam et al., 2014). In addition, broader features of the peer group, such as popularity, become increasingly valued (LaFontana and Cillessen, 2010) and can play a role in shaping goals and behavior (Crone and Dahl, 2012). Given the heightened complexity and salience of adolescents' social environments, researchers often rely on methods such as social network analysis, which can operationalize numerous features of adolescents' peer relationships.

Social network analysis refers to the method of measuring the

² While we identify candidate regions associated with these neural processes, it is important to note that these three general psychological processes are not restrictive, and functional connectivity between regions are theorized to contribute to multiple processes. For example, the amygdala's role in both social cognition and social motivation functional networks is related to social network size and complexity (Bickart et al., 2014).

structure of social relationships between multiple individuals³ in a social environment. In the context of developmental psychology and neuroscience research, this approach often focuses on a child or adolescent's peer network, with a particular focus on school-based networks. In social network analysis, researchers collect information about the relations (referred to as edges or ties) between individuals (referred to as actors or nodes in the network) in a defined social environment (such as a classroom, extracurricular group, or dormitory). While friendship is one of the most common edge types in adolescent social network research, edges could constitute any type of relation between adolescents and their peers. Previous studies of adolescent development have examined edges related to social status (nominations of popularity and social preference), victimization (disliking and bullying), social support (feelings of trust or instances of disclosure), and communication (contacts via texting, calling, or social media) (reviewed in Neal, 2020). The majority of social network studies discussed in this review focus on individuals' friendship networks amongst their peers (e.g. classmates for adolescents in middle and high school, individuals who share a dorm in undergraduate institutions, people in the same club or village amongst adults). Thus, we will use the term "peer networks" to describe the friendship structures that exist in adolescents' social environments (most commonly their schools), and "social network" to describe the data that measures those structures.

Different methodological choices during the collection and analysis of social network data influence the type of data measured and the inferences that can be drawn. These choices include, but are not limited to, (1) whether data is collected from focal individuals about relations between local individuals in their environment (egocentric networks) or collected from as many individuals as possible in a bounded group about their relations to all other individuals (sociocentric networks), (2) whether ties need to be reciprocated (e.g. both person A and person B nominate each other as friends), and (3) whether ties should be binary (a tie exists or does not) or weighted (the tie indicates the strength of the relationship). Moreover, different person-level measures of degree and centrality, a network measure that represents an individual's level of connectedness to others, provide different information about an individual's relative position or influence in a social group (see supplement for more details). For example, sociometric popularity, a measure of social status that is particularly valued and impactful in early adolescence (LaFontana and Cillessen, 2010) is often calculated as a z-score of in-degree (the raw number of nominations an individual receives from others) for popularity nominations (Prinstein, 2017). While this review focuses on varying features and applications of social network analysis that may be relevant for developmental neuroscience research, it does not constitute an introduction to the methodology. We provide a brief introduction to methodological considerations in the supplement, and recommend Baek et al. (2021) for a more detailed discussion of social network methods, definitions, and limitations. Overall, social network analysis is a powerful tool to capture relevant features of adolescents' social environments that are relatively under-explored in developmental neuroscience research.

3. Adolescent neurodevelopment

Adolescence is a period of significant neural, biological, and social change, resulting in a developmental window distinct from childhood and adulthood (Blakemore and Mills, 2014). Structural and functional changes in the brain are implicated in the unique characteristics of adolescents' social goals and behaviors. Concurrently, factors such as school transitions, increased participation in extracurricular activities, and greater access to social media drive a rapid expansion of

³ While SNA usually focuses on the relations between individual people in a network, actors in social network analysis could also be groups (e.g., neighborhoods, clubs, businesses, etc.).

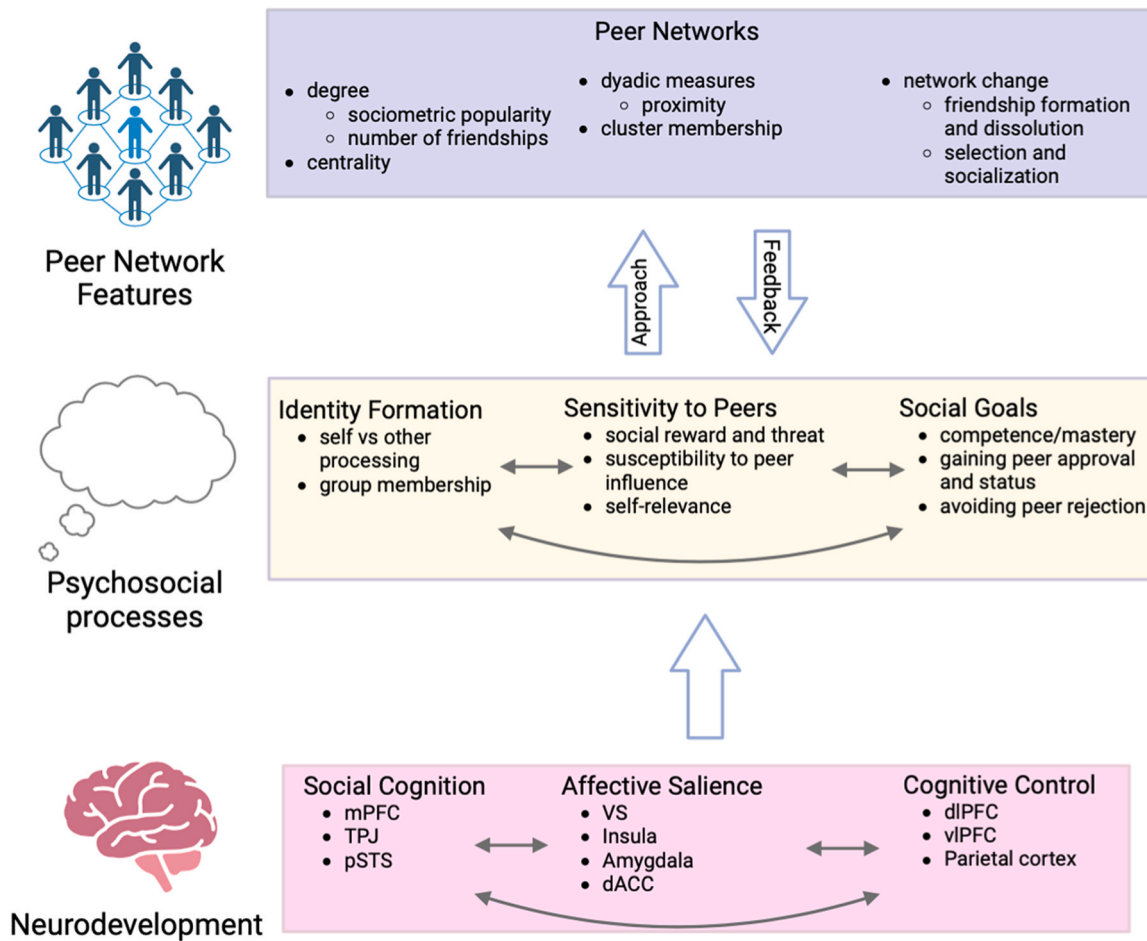


Fig. 1. A conceptual framework for the interrelations between relevant features of adolescent development when integrating neurodevelopment, social networks, and psychosocial processes. Neural systems most often related to social processes, including brain regions implicated in social cognition, affective salience, and cognitive control, interact with one another to contribute to interrelated psychosocial processes, such as identity formation, sensitivity to peers, and social goals. These, in turn, are related to how individuals approach and interpret feedback from their changing social networks. Thin gray arrows represent interactions and relations within levels of the model, whereas larger blue arrows represent relations across levels. For the neurodevelopment layer, bullet points represent some of the individual regions in the network, whereas bullet points in the other layers represent potential subconstructs that could be operationalized for measurement.

adolescents’ social environments. Studying the unique facets of adolescent neurodevelopment can significantly contribute to our understanding of how individuals perceive and interact with their complex social worlds. In particular, we briefly discuss the relevant neurodevelopmental features of adolescents’ self and other processing, sensitivity to peer contexts, and social goals, and subsequently consider the relevance of broader peer contexts and how social network analysis can enrich our understanding of these processes. For more exhaustive reviews of the developing brain in relation to these concepts, we recommend Crone and Fuligni (2020), Schriber and Guyer (2016), and Crone and Dahl (2012), respectively.

3.1. Identity formation

Self and Other Processing. Developing a stable sense of self and considering how one fits into their social world is a key developmental task in adolescence (Pfeifer and Peake, 2012). In adolescence, questions of the self, such as “Who am I?” and “What do I think of myself?” are inherently intertwined with thoughts of others, such as “What do others think of me?” and “Where do I fit in?”. This entanglement of self-identity and consideration of others is theorized to be driven by numerous factors, including cognitive improvements in mentalizing and perspective taking (Pfeifer et al., 2009) and increased access to peer networks and association with social groups (Blakemore and Mills, 2014; Rubin et al.,

2007). Developmental neuroscience research has explored the relationship between the self and other-oriented development in adolescence, establishing that a common network of brain regions is recruited for the cognitive and social processes underlying the consideration of the self and others (reviewed in Crone and Fuligni, 2020; Denny et al., 2012; Pfeifer and Peake, 2012).

Theories of identity development in adolescence often focus on the medial prefrontal cortex (mPFC), considered to be a key hub for integrating information about the self and others (Crone and Fuligni, 2020), as well as the ventral striatum (VS) and regions associated with mentalizing (often deemed the “social brain” or “social cognition” network) including the temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), and posterior parietal cortex (including the precuneus and posterior cingulate cortex (PCC)). Developmental studies from childhood to adulthood have identified both linear and quadratic changes in the recruitment of the mPFC and related regions during various mentalizing and perspective taking tasks. For example recruitment of the mPFC during mentalizing and social decision making decreases from adolescence to adulthood (reviewed in Blakemore, 2008, 2012), whereas recruitment of the TPJ and pSTS is greater in adulthood (Blakemore et al., 2007; van den Bos et al., 2011). Other studies have highlighted quadratic patterns of functional development, with peaks in activation in the mPFC in mid adolescence, particularly with respect to the evaluation of the self and similar or dissimilar others (van Buuren

et al., 2022) and social evaluations from others (Somerville, 2013). Overall, these studies highlight two relevant developmental trends. First, when mentalizing and making social decisions, adolescents recruit regions involved in social cognition differently than adults, which has been theorized to be driven by greater overlap between conceptions of the self and others in adolescence, followed by increasing individuation into adulthood (Pfeifer and Peake, 2012). Second, evidence of quadratic trajectories, wherein task-related functional activation during mentalizing and social evaluation paradigms peak in mid-adolescence (peaking around 14 years in van Buuren et al., 2022, and 15 years in Somerville, 2013), corroborate theories that, more so than adults and children, adolescents are sensitive to social information and its relation to the self.

Incorporating Broader Peer Contexts. When considering how the aforementioned findings are relevant for understanding adolescents' peer networks, it is important to understand how neural processing differs depending on who the "other" is. Numerous characteristics of an individual peer may influence the degree to which an adolescent values or considers the peer's perspective. For example, when making trait judgments about others, studies have found differential vmPFC functional connectivity and dmPFC activation for similar versus dissimilar peers (van Buuren et al., 2020, 2022), and heightened vmPFC activation for friends versus other familiar individuals, such as teachers (Romund et al., 2017). While these studies rely on the participants' nomination of a few candidate peers, social network data from larger social groups could allow researchers to expand these designs to other salient social features, such as popularity or friend group membership.

Additionally, there is evidence that relations between neural processing of the self and others are likely context dependent. For example, mPFC activation during trait judgments was heightened when the domain of information was aligned with the "other" (e.g. parents for academic statements, friends for social ones, Pfeifer et al., 2009), and adolescent participants exhibited heightened VS activation when considering how their best friends considered themselves specifically for social traits, relative to academic or physical ones, (Jankowski et al., 2014). Given that adolescence is often a period where adolescents begin to identify with multiple social groups (Kang and Bodenhausen, 2015; Turner et al., 1987), future work should identify the contexts in which adolescents identify with or consider their peers' perspective. Social network methods such as cluster analysis, wherein friendship groups are algorithmically determined from social network data (Tabassum et al., 2018), or social identity mapping, wherein participants self-identify social groups, their influences, and their interrelations with one another (Cruwys et al., 2016) could provide greater detail on how subgroups and identities embedded in the larger peer network may be related to the developing social brain.

3.2. Sensitivity to peers

Neurobiological Sensitivity to Social Contexts. Adolescence is a developmental window characterized by an increased orientation toward social cues and peer contexts. This tenet has been explored in numerous developmental neuroscience studies, including those that evaluate neural systems related to reward, social cognition, attention, and affective processes (reviewed in Crone and Dahl, 2012; Foulkes and Blakemore, 2016; Mills et al., 2014; Nelson et al., 2016). However, recent theories of neurobiological sensitivity to social contexts suggest that not all adolescents are sensitive to their social environments, but that this sensitivity depends on neurobiological sensitivity (Schriber and Guyer, 2016). These theories, based on previous differential susceptibility frameworks (Belsky et al., 2007; Ellis et al., 2011), posit that individuals vary in how sensitive they are to environmental input, and such variation can be captured by examining differences in neural activation and connectivity of relevant socio-affective regions (Do et al., 2020; Schriber and Guyer, 2016). Examining the moderating role of these neural systems has become a powerful tool for understanding the complex interactions between adolescents' neurodevelopment, their

social environments, and potential behavioral outcomes. For example, individual differences in neural sensitivity (greater VS activation to social rewards and punishments (Telzer et al., 2021); and greater connectivity within the affective salience network (Do et al., 2022) moderates the relationship between perceived peer norms and adolescents' own behaviors, suggesting that this neural sensitivity could reflect individual differences in susceptibility to peer influence.

Incorporating Broader Peer Contexts. Given the multitude of ways that social network analysis can capture features of adolescents' social contexts, and the breadth of mechanistic information provided by well-designed neuroimaging paradigms, utilizing these within a neurobiological susceptibility framework could be a powerful means of assessing individual differences in adolescent outcomes. For example, with sufficient network coverage, researchers could introduce individuals' neural sensitivity data to different methods that model network change, such as diffusion models, which test how attributes of actors influence the spread of behaviors in a network (Valente, 2005). These integrations could help to test whether individual neural factors, such as sensitivity to social rewards, social threats, or peer evaluations, predict whether actors are more susceptible to peer influence effects. Alternatively, they could be applied to predicting risk for psychopathology, assessing which individuals are at greatest risk for experiencing negative outcomes as a result of network characteristics such as social isolation, friendship instability, or social status loss. Lastly, as we will discuss later, different social network measures, such as sociometric popularity (measured as one's relative number of popularity nominations compared to their peers), can be implemented into fMRI tasks to assess how sensitivity to broader network features such as social status may also be related to behaviors and outcomes. Overall, social network analysis could allow researchers to expand the breadth of which local and global features of adolescents' social environments may interact with their individual neural sensitivities to social stimuli.

3.3. Social goals

Flexible engagement of neural systems related to social goals. While adolescence is generally understood to be a time wherein peers are more salient and thus exert greater influence on individuals' behaviors, recent neurodevelopmental theories assert that adolescents maintain the ability to flexibly recruit cognitive control in line with their social goals (Crone and Dahl, 2012). Although regions associated with cognitive control undergo relatively protracted structural development, leading to poorer cognitive control than adults in some domains (Somerville and Casey, 2010), there are instances wherein adolescents exert better cognitive control than adults (reviewed in Crone and Dahl, 2012; Telzer et al., 2022). Such performance and flexibility is theorized to result from increased motivational salience and sensitivity to environmental contexts (Davidow et al., 2018), which may be particularly relevant when considering how neural systems are engaged in relation to social goals.

When considering how adolescent neurodevelopment interacts with their complex peer networks, it is useful to consider the broad social goals that individuals may rely on to guide their social behavior. Social achievement goal theory (Ryan and Shim, 2006) posits that individuals are motivated to engage with their peers by three categories of goals. These goals include mastery, which consists of increasing competence in social skills, performance-approach, which consists of gaining social status and peers' approval, and performance-avoidance, which consists of efforts to minimize peer disapproval and rejection. Research evaluating the neural correlates of different social goals suggests that reactivity and functional connectivity among regions involved in social-affective processing and cognitive control, both at rest and during experiences of positive and negative feedback, differs based on social goal endorsement. For example, higher endorsement of avoidance goals is related to heightened amygdala-medial temporal gyrus (MTG) connectivity when experiencing negative feedback, suggesting that that

amygdala connectivity may buffer attunement to socially threatening feedback amongst those who are most concerned with avoiding rejection (Davis et al., 2023). In contrast, higher endorsement of performance-approach goals is associated with lower sensitivity to negative and positive feedback in social regions such as the TPJ, pre-cuneus and PCC. These findings might be associated with social strategies that, amongst youth who prioritize gaining status, emphasize appearing socially competent rather than those that incorporate peer feedback (Davis et al., 2023). Research that has focused on full goal profiles, rather than social goals in isolation, has also identified differences in functional connectivity. Denser connectivity among numerous cognitive control and social-affective regions is related to goal profiles characterized by higher endorsement of all three social goals, although these do not predict differences in outcomes such as psychopathology (Pelletier-Baldelli et al., 2023).

Incorporating Broader Peer Contexts. While these studies provide preliminary information about the neural mechanisms that support social goals, social network analysis could complement these findings to provide a more comprehensive understanding of individual differences in outcomes across social goal profiles. Depending on the types of nominations collected, social network analysis could offer greater detail into whether individuals progress toward these goals. For mastery goals, metrics from friendship networks such as out-degree (the number of friendships an individual participant nominates) and in-degree (the number of individuals who consider the focal participant a friend) could inform researchers about the friendship perceptions of the participant and their peers, respectively, which may both be relevant for understanding one's social competency. The degree to which individual friendship nominations are reciprocated may also be of use in understanding social competency, since reciprocated friendships are considered stronger and more reliable (Vaquera and Kao, 2008). For performance goals, nominations related to liking, disliking, and popularity (Prinstein, 2017) could indicate whether an individual is broadly accepted or rejected by their peer group. Pairing self-reported social goals with more quantifiable metrics of social connectedness could allow researchers to better understand the outcomes associated with different goal profiles. For example, while functional connectivity in relation to social goals was not predictive of psychopathology in the aforementioned neuroimaging study, it may be the case that these relations depend on whether one has actually met their social goals.

4. Insights and implications from current research

While the proposed framework identifies the constructs and neural systems we consider most relevant for understanding the relations between neurodevelopment, peer network features, and psychological processes, there are certainly other constructs that are relevant for social and developmental research for adolescents. Nonetheless, this framework provides a foundation for understanding current research using these methods, as well as a promising starting point for researchers interested in utilizing these methods to thoroughly study adolescent social development. In this section, we will address some of the most recent research on neurodevelopment and social networks, noting when our framework can be utilized to understand and expand upon this research. In particular, we will focus on three categories of findings. First, we will discuss how neural structure and function have been related to connectedness within social networks. Then, we will highlight studies that probe how individuals perceive features of their social networks at the neural level, with a particular focus on popularity sensitivity in early adolescence. Lastly, we will focus on innovative studies that utilize measures of neural similarity to contribute to our understanding of social network proximity and connectedness in adolescents and young adults.

4.1. Neural structure and function are associated with social network structure

Evolutionary theories of human development hold that human neuroanatomy evolved to support humans' complex social lives (Humphrey, 1976). Motivated by these theories, studies (mostly in adult samples) have identified that differences in both the structure and function of the brain can relate to individual network characteristics, such as self-reported friendship network size (Bickart et al., 2011; Kanai et al., 2012; Lewis et al., 2011; Noonan et al., 2018; Von Der Heide et al., 2014). However, these studies focus on either out-degree in egocentric networks (i.e., the number of friends an individual recalls freely or through a structured scale), which may be subject to bias from individuals' perceptions, or friendship number in online networks, which may not sufficiently capture social network complexity or friendship quality (Dunbar, 2012). Recently, researchers have paired neuroimaging methods with additional network analysis methods to evaluate how the brain is related not only to network size, but also other network features such as constraint (a measure of brokerage, measuring the degree to which an individual connects otherwise unconnected people or groups), eigenvector centrality (the degree to which an individual is connected to well-connected others), and density (how well connected one's friends are to each other) (Hyon et al., 2022; Schmäzle et al., 2017). By probing multiple features of social networks, these studies provide more detailed information about how the brain is associated with more complex social engagement.

In a young adult sample (ages 24–35) patterns of white matter tracts in social and affective networks, as measured using diffusion tensor imaging (DTI), were predictive of network characteristics such as constraint and eigenvector centrality, but not the number of friendship nominations participants sent or received (out-degree and in-degree) (Hyon et al., 2022). Interestingly, no white matter tract alone was predictive of centrality, indicating the importance of evaluating how multiple neural systems jointly contribute to social network characteristics. The features and correlates of constraint and eigenvector centrality can expand our understanding of the link between neural factors and social network attributes. For example, individuals with high levels of constraint are usually socially adept and flexible, able to engage with different groups and monitor their behaviors within them accordingly (Oh and Kilduff, 2008). High eigenvector centrality is also a consequence of social competence, and could reflect both an ability to effectively maintain social ties as well as navigate social hierarchies. Thus, strengthened white matter integrity in social and affective networks may support these social skills (Hyon et al., 2022). However, the direction of effects cannot be inferred - it may also be that, by virtue of being in these social network positions, individuals must engage in social skills that modulates their neural structure over time. Longitudinal work, as well as study designs that employ behavioral mediators or functional imaging, can contribute to our understanding of the mechanisms linking neural features to social network positionality.

It is important to note that most of the studies to date have included adult samples, or included both adolescents and adults (e.g. Hampton et al., 2016; Von Der Heide et al., 2014, participants aged 12–30). Given the significant changes in neural structure and function (Blakemore and Mills, 2014) and the dynamic nature of peer networks (Cotterell, 2013) during adolescence, future work should target different developmental windows to better understand how neurodevelopment and social structures co-develop across the lifespan. For example, previous work linking white matter development and self-reported network size found that both increase with age across adolescence and young adulthood (Hampton et al., 2016, sample ranging from 12 to 30 years old), highlighting the need to evaluate the dynamics of these processes throughout development.

A study amongst adolescents (16–17 years old) probed the relations between density in online networks and functional connectivity in networks associated with social cognition and "social pain" during

experiences of rejection in the Cyberball paradigm (Schmälzle et al., 2017). Heightened functional connectivity between the left and right TPJ during rejection was associated with less dense online networks, such that these participants' friends were less likely to be friends with one another. It may be that when rejected, those with less dense networks increasingly engage the TPJ, a brain region involved in mentalizing and social cognition, given the less supportive, close-knit nature of their networks (Schmälzle et al., 2017). Alternatively, heightened TPJ activation during rejection may be associated with behaviors that predispose adolescents to become situated in less dense networks. Nonetheless, by utilizing network density, these findings provide more thorough information on the social environments associated with heightened rejection sensitivity. Rejection sensitivity, which is commonly associated with social outcomes throughout adolescence (Gao et al., 2017; Vijayakumar et al., 2017), relates to features of our framework such as peer sensitivity and social goals. Our framework points to other means by which neural function might be related to social network structure. For example, social reward sensitivity is considered to contribute to overall approach behaviors and social engagement (Fareri and Delgado, 2014; Radke et al., 2016; Simon et al., 2010), indicating potential roles for neural regions and circuits related to reward and motivated behavior.

4.2. Neural tracking of social status in adolescence

Understanding the neural processes by which adolescents perceive features of their peer networks can help us understand the ways individuals navigate these networks and form connections. One feature of peer networks, social status (i.e., the number of popularity or liking nominations an individual receives relative to their peers), is particularly salient among adolescents (LaFontana and Cillessen, 2010; Prinstein, 2017), and is often associated with individuals' social goals and behaviors (Crone and Dahl, 2012; Gommans et al., 2017). Thus, researching how the brain encodes social status in adolescence is a promising first step in understanding how adolescents' social network cognition relates both to social network outcomes and related social behaviors.

While numerous studies have probed the cognitive processes involved in social status detection (reviewed in Koski et al., 2015), only a handful of studies have examined social status detection at the neural level. Such studies conducted amongst older adolescents (Morelli et al., 2018) and young adults (Parkinson et al., 2017; Zerubavel et al., 2015) indicate that regions related to social cognition, including the dmPFC, precuneus, and TPJ, affective salience, including the vmPFC, ventral striatum, and amygdala, and cognitive control, including the vlPFC spontaneously encode information about the social status or centrality of participants' peers during passive face-viewing tasks. In one study, researchers used social preference, a social status index generated by the number of likeability nominations in one's peer network, as a parametric modulator to examine how early adolescents track social status in their peer networks. Results indicated that adolescents encoded both the highest and lowest status peers in the fusiform face area (FFA) (Dai et al., 2023). In contrast, adolescents differentially encoded high and low status peers in the dorsolateral prefrontal cortex. These regions differ from those in adults (e.g., Zerubavel et al., 2015) and may be the result of developmental changes in how individuals encode social networks, the result of methodological differences between the studies (Zerubavel et al., 2015 evaluated peers across the entire continuum of social status, whereas Dai et al., 2023 evaluated peers at ± 1 standard deviation from the average level of status), or from differences in neuro-hemodynamic coupling (Schmithorst et al., 2015). These findings demonstrate the need to further investigate how adolescents encode social status and other salient features of their networks.

Individual differences in how adolescents encode social status may have potential downstream impacts on social behaviors. Indeed, early adolescents who exhibit greater sensitivity in the dmPFC to their most

popular peers are more likely engage in greater risk-taking behaviors over the course of one year (Capella et al., 2023). Popular teens tend to engage in greater risk taking in adolescence (Gibbons et al., 2003; Mayeux et al., 2008). Thus, heightened sensitivity to popular peers in the dmPFC may impact how adolescents approach and behave in their social networks. For example, it may be that heightened dmPFC sensitivity to popularity drives individuals to befriend more popular peers, which increases opportunities for risk taking, as popular teens tend to engage in greater risk taking. Alternatively, heightened dmPFC sensitivity to popularity may increase risk-taking behavior in an attempt to follow social goals and gain status (Gibbons et al., 2003). Overall, these possibilities highlight the utility in applying our framework toward studying adolescent social development.

4.3. Neural similarity and social networks

Social networks are not only comprised of the individuals within them, but also the relationships between these individuals. Thus, while the aforementioned studies highlight the utility of researching how an individual's brain orients them toward their social environment, it is also important to consider how similar and dissimilar neural responses across individuals relate to social network features. Recent studies in adults have employed innovative methods to evaluate how neural similarity (i.e., how similar two individuals' brains respond to the same stimuli) and neural idiosyncrasy (i.e., how different one's neural response is from all others measured in their network) relate to measures of connectedness, such as proximity (Hyon, Kleinbaum, et al., 2020; Hyon, Youm, et al., 2020; Parkinson et al., 2018) and centrality (Baek et al., 2022), in the social networks.

Similarities amongst friends, whether it be in demographic characteristics, personality traits, emotional experiences, and behaviors, is a common phenomenon within social groups. (McPherson et al., 2001). Research in young adults (ages 25–32) has found that similar neural responses to audiovisual stimuli or at rest predict proximity among dyads, such that those closer together in a friendship network have more similar neural responses (Hyon, Kleinbaum, et al., 2020; Parkinson et al., 2018). Given that neural similarity between individuals can underlie similar interpretations of stimuli (Lahnakoski et al., 2014; Nguyen et al., 2019), higher neural similarity amongst friends and those close together in friendship networks may suggest that individuals are more likely to be affiliated with those who, on a neural level, perceive and interpret the world more similarly. Such similarity might arise from selection, wherein individuals preferentially select people similar to themselves as friends, socialization, wherein individuals become more similar to their friends over time, or shared external causation (Shalizi and Thomas, 2011)

Research in an early adolescent sample (ages 11–13) suggests that these results may also extend beyond domain-general neural processes (i.e., audiovisual stimuli and resting state fMRI) to more specific ones, such as the processing of affective stimuli or cues from social contexts that are relevant for individuals' social interactions in their networks. Given that emotions and mood states are subject to socialization and selection processes in adolescents (Block and Burnett Heyes, 2020; Elmer et al., 2017), and are particularly relevant for adolescents' social experiences and outcomes in general (Klimes-Dougan et al., 2014), evaluating neural similarity of affective processing is a promising approach to probe how neural similarity may be related to social network proximity during this stage of development. Indeed, neural similarity in vmPFC response to positive and negative stimuli was associated with network proximity across multiple middle school peer networks (Feldman, Capella, et al., in review). These results suggest that shared representation of emotional experiences, particularly via socio-affective regions that underlie emotional meaning-making and affective experience (Fox et al., 2018; Roy et al., 2012), could be an important factor in the formation and maintenance of friendships throughout adolescence and early adulthood. However, a key limitation

in these studies is that the direction of the relationship (i.e., whether it is selection, socialization or shared external causation) is unclear. While adolescents and adults may be more likely to socialize and maintain friendships with those who have similar neural responses (i.e., selection), it is also possible that friends' neural responses become more similar as the relationship unfolds (i.e., socialization). Thus, longitudinal work is necessary to better understand these processes, particularly in adolescence when both neural function and peer networks undergo substantial reorganization and change.

Another network-focused approach to relating individuals' neural responses to one another consists of efforts to probe the consequences of similarity, or lack thereof, to the network as a whole. Since neural similarity to an individual is associated with a higher likelihood of having a friendship or close proximity to that individual, it follows that being similar, on average, to multiple others in the network should facilitate greater connectedness overall, which could be measured by network centrality. Indeed, recent work amongst an older adolescent sample (ages 18–21) established that individuals who are highly central in their friendship networks have more similar neural responses to all others in their network (as measured by an average of dyadic similarity to each measured individual) in regions of the "social brain" such as the dmPFC and precuneus (Baek et al., 2022). Additionally, the inverse is also true – those with low centrality have more idiosyncratic neural responses than other members of the network. Moreover, individuals on the peripheries of their networks are not more similar to other individuals with low centrality, suggesting that these individuals are each "dissimilar in their own idiosyncratic way" (Baek et al., 2022). These results suggest that sharing patterns of neural activity with group members could facilitate overall network connectedness, which are also associated with a wide variety of social and psychological benefits (Morelli et al., 2017; Ueno, 2005), whereas idiosyncratic neural responses may be a risk factor for low centrality. Given that low centrality is generally associated with a variety of negative outcomes, particularly in adolescence, it may be the case that greater neural idiosyncrasy is a risk factor for such outcomes. However, once again, longitudinal designs are needed to infer causality, and carefully designed studies should be implemented to probe how neural similarity and social network connectivity are related to positive or negative outcomes.

5. Future considerations and directions

Given the numerous measures and methodological decisions associated with SNA, researchers are tasked with determining which network features may be most relevant to their theories and hypotheses. For example, different measures of centrality in friendship or status networks provide different information about one's level of influence or connectedness in the peer group – eigenvector centrality is often utilized to gauge how well connected one is to other influential actors, whereas betweenness centrality and constraint often assess how well one can connect to multiple subgroups or transmit information between subgroups in social contact or communication networks (see supplement and Baek et al., 2021 for more details on individual measures of centrality). Rather than choosing individual metrics, researchers could also test multiple measures of degree and centrality (and correct for multiple comparisons, e.g. Hyon et al., 2022) or rely on factor approaches to reduce measurement error and capture broader constructs like social integration and status (Cole et al., 2018). Such approaches could facilitate easier comparisons across studies and improve researchers' ability to draw inferences across the field. Other methodological decisions could be motivated by the unique features of peer relationships in adolescence. For example, while eigenvector centrality is commonly utilized to operationalize positions of social influence in adult populations, it may be more appropriate to focus on dimensions of social status that are salient and valued in adolescence (particularly early adolescence) such as sociometric popularity (LaFontana and Cillessen, 2010).

While current research provides compelling insights on relations between the developing brain and social outcomes and behaviors, they only scratch the surface of the possible applications of integrating neuroimaging and social network data. As developmental neuroscientists increasingly turn to social network analysis to capture social information spanning participants' entire networks (Baek et al., 2021), it is critical to pursue research that is both rooted in theory and addresses the contexts and challenges that adolescents face in modern society, such as higher rates of psychopathology (Benton et al., 2021), and changes in social interactions within digital contexts (Nesi et al., 2018). Proper integration of neuroimaging, behavioral, and social network data can enable researchers to more completely understand the health outcomes and behavioral trajectories of adolescents across varying social, digital, and cultural contexts.

5.1. Understanding behavioral and health outcomes

While adolescence is often framed as a period of increased risk for psychopathology and negative risk-taking behaviors, it also a developmental window that affords individuals the ability to establish or maintain positive behavioral trajectories, including growth in domains such as prosociality, social exploration, individuation, and autonomy (Telzer et al., 2022). Common developmental theories related to behavior and well-being, such as differential susceptibility models, posit that outcomes are the result of interactions between individual biological factors and social contexts (Schriber and Guyer, 2016). In line with these theories, researching predictors for positive and negative adolescent outcomes, as well as identifying potential targets for intervention, requires studying the mechanisms of interactions between biological factors, such as neural structure and function, and social contexts, such as the characteristics of one's peer network.

Utilizing neuroimaging data and social network analysis could provide researchers with novel approaches to understanding how adolescents' neurobiology interacts with their social environments to influence outcomes. For example, behavioral research supports the notion that low popularity is a risk factor for depressive symptoms or externalizing behaviors, but that this relation is moderated by whether an individual values social status as a goal to be obtained (Prinstein and Aikins, 2004; Shoulberg et al., 2011; van den Broek et al., 2016). As discussed in this review, social status sensitivity (Capella et al., 2023; Morelli et al., 2018; Parkinson et al., 2017; Zerubavel et al., 2015) and goal orientation (Davis et al., 2023; Pelletier-Baldelli et al., 2023) are supported by all three neural systems in our framework. Thus, future work could focus on these psychosocial processes when evaluating the neurobiological factors that differentiate which low status adolescents are most at risk for psychopathology or other negative outcomes. This is just one of many possible applications of our framework - future studies could utilize the breadth of neuroimaging designs and social network data to understand a multitude of positive and negative outcomes.

It is important to note that differential susceptibility models are not the only way to conceptualize behaviors in the social setting. As outlined in our framework, behaviors can also arise from the way adolescents approach the network or react to feedback from it. For example, increased risk-taking associated with heightened neural sensitivity to popularity (Capella et al., 2023) may be an approach behavior (as a means of gaining status) rather than a consequence of one's network position. Moreover, differential susceptibility models are limited when utilizing social network analysis to predict behavioral and health outcomes because one's position in a network is determined in part by these behaviors. For example, there is evidence for both selection and socialization effects for internalizing symptoms (reviewed in Neal and Veenstra, 2021), highlighting that these symptoms can be both a precursor and an outcome of one's friendships and network position. Longitudinal network methods, such as SAOMs (see supplement for more details), can better capture the dynamic nature of social networks to accurately assess the interplay between behavior, health, and networks

throughout adolescence.

5.2. Exploring digital social contexts

As social media use has become nearly ubiquitous among adolescents, researchers and the public alike have become increasingly interested on the impacts these new digital contexts may have on adolescent development. Unique characteristics of social media, such as increased quantifiability, publicness, and availability of peer interactions, may heighten or alter the impact of processes that already occur amongst adolescents, such as peer victimization, peer influence, and status hierarchies (Nesi and Prinstein, 2019). Moreover, the effects of social media use are not monolithic – social media can increase negative outcomes such as depressive and anxious symptoms in some youth while offering benefits such as exploration, creativity, and expression for others (reviewed in Best et al., 2014; L. Hur and Gupta, 2013; Orben and Przybylski, 2019). Thus, research into social media's impact on adolescent social development should address two goals. First, it should consider the mechanisms behind how social media's unique features transform peer experiences and networks. Second, studies should evaluate how these transformed social interactions are differentially experienced across youth – assessing which psychological and neural differences predispose individuals for positive or negative outcomes.

Studies that integrate neuroimaging and social network analysis are well suited to meet these goals. As discussed in the previous sections, neuroimaging studies grant the ability to assess individual differences in susceptibility to social contexts, whereas social network analysis allows for capturing broader features of these social contexts. One study in adolescence encapsulates these advantages quite well – finding that neural sensitivity to popular peers in adolescents' peer networks moderates the link between social media use and daily affect (Maza et al., 2023). By identifying neurobiological sensitivity to popularity, via vmPFC and dmPFC activation in response to highly popular and unpopular peers, this study identifies individual differences predicting which adolescents will benefit or face risks from social media use. Furthermore, by focusing on sensitivity to status, the study suggests that features of social media related to popularity, such as quantifiability, publicness, and visualness (Nesi and Prinstein, 2019) may be particularly impactful for youth with heightened neural sensitivity to status cues. Similar innovative study designs can provide critical information on how adolescents navigate increasingly prevalent social media contexts.

5.3. Incorporating cultural and social identities

While sociocultural factors play a large role in shaping adolescents' social development and behaviors, remarkably little research has evaluated how findings from developmental neuroscience may vary across cultures (Qu et al., 2021). Most of the aforementioned findings are among U.S. or other Western samples, and cultural differences in either neurodevelopmental processes, social network structures, or behavioral norms could induce variation across different groups. For example, research has identified cultural differences in many of the behavioral themes discussed in this review, including prosocial behavior, peer influence processes, and risk-taking (reviewed in Telzer et al., 2022). Even adolescents' perceptions of their networks can differ by culture, leading to differences in the way individuals orient to their networks and seek social support (Harrison et al., 1995). Given these differences, developmental and social neuroscientists should not take the generalizability of their findings for granted when utilizing neuroimaging and social network data.

Even within Western countries that are overrepresented in neuroscience research, adolescents interact with peers from varying cultural, racial and ethnic backgrounds. Given that neurodevelopmental changes, particularly in the mPFC and other "social brain" regions, support the increased relevance of others to self-identity in adolescence (Pfeifer and

Peake, 2012), it is critical to assess how interactions with peers of varying backgrounds impacts identity development and, in turn, social behavior. The influence of other social identities, such as smaller subgroups generated from activities, neighborhoods, or schools, are also understudied in neuroscience research, and could be probed further using community detection or social identity mapping methods.

6. Conclusion

This review discusses how the unique features of adolescent neurodevelopment scaffold the psychosocial processes that influence social and behavioral outcomes and potential bidirectional associations. Developmental changes in neural circuits related to social cognition, affective salience, and cognitive control have all been implicated in the unique psychosocial behaviors amongst adolescents, including greater incorporation of peers into self-identity, heightened sensitivity to social stimuli, and increased focus on pursuing social goals. These, psychological processes in turn, shape and are shaped by the ways in which adolescents orient toward their networks and interpret feedback from these social contexts. Moreover, dynamic interactions between individual neural factors and the social environment can induce variation in adolescent outcomes, such that adolescents are at heightened risk for negative outcomes, but also capable of establishing lifelong positive trajectories. While these processes are broad and complex, neuroimaging and social network analysis can effectively complement one another to provide in depth information about individual neurobiological characteristics and features of adolescents' broad social environments.

CRedit authorship contribution statement

Eva H. Telzer: Writing – review & editing. **Jimmy Capella:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dcn.2024.101442](https://doi.org/10.1016/j.dcn.2024.101442).

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